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# Life history of two new species of *Prorops* (Hymenoptera, Bethylidae) ectoparasitic on adult *Hypothenemus eruditus* beetles (Curculionidae, Scolytinae) in Hawai'i

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## Abstract

Aspects of the life history and biology of two *Prorops* spp. are explored, *Prorops maya* **sp. nov.** and *Prorops umiehu* **sp. nov.** Aspects of their behavior are deduced through dissection of plant material and through the use of "phloem sandwich" style observation chambers. Both were found to be ectoparasitoids of adult *Hypothenemus eruditus* beetles. They thus show a novel feeding behavior as, along with a *Plastanoxus* sp., the only bethylids known to parasitize the adult stage of their hosts, and the only known ectoparasitoids of adult scolytids. Searching, stinging, host feeding, and oviposition behaviors are reported and illustrated with photographs and video. Oviposition occurs on the ventral side of the membraneous region between the pro- and mesothorax of the beetle, and larvae feed through this location. The projection on the frons, a defining character of the genus *Prorops*, is observed to function as a tongue and groove mechanism with which the adult female pushes on the edge of the prothoracic sclerite of the host beetle while maintaining use of its mandibles to chew on the membrane underneath for host feeding and in preparation for oviposition. Defensive action of a *Hypothenemus* sp. against the wasp's sting by clamping down on the intruding ovipositor between its pro- and mesothorax is also reported, though this behavior was only observed once and thus its generality is uncertain.

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**Keywords**
Functional morphology, host defense, macadamia, parasitoid Hymenoptera, Scolytinae

## Introduction

There are currently eleven known species in the genus *Prorops* (Hymenoptera: Bethylidae), including the two described here. Members of this genus can be distinguished from other members of Scleroderminae by having a distinct snout, a projection of the anterior part of the frons that is either a singular projection with a median groove, or is separated into two distinct projections on either side (Azevedo et al. 2018). A list of previously described species is provided below. Location records were obtained through reports in published literature, so there may be specimens collected from other places that are not noted here:

### *Prorops impotens* Waichert & Azevedo, 2012

Known from Madagascar. No recorded hosts.

### *Prorops mandibularis* Lim & Lee, 2011

Known from Central Cardamom, Cambodia. No recorded hosts.

### *Prorops nasuta* Waterson, 1923

A parasitoid of *Hypothenemus hampei* (Ferrari, 1867), the coffee berry borer. *Prorops nasuta* has been imported from its native range in Africa to much of the coffee growing world as a biological control agent. It enters coffee berries, host feeds on all immature stages, stings and paralyzes the adult stage, and is an ectoparasitoid on the pupal and late instar larval stages (Infante et al. 2005). It is thought to be native to parts of Central and East Africa including Uganda, the adjacent northwest part of Tanzania, the DRC, and parts of West Africa (Le Pelley 1968). It has been released as a biocontrol agent in South and Central America, southern Asia, and Indonesia (Vega et al. 2015). In addition to the coffee berry borer, this species was also recorded emerging from *Hypothenemus seriatus* (Eichhoff, 1872) in Jamaica (Evans 1977), and is reported to attack and develop on *Caulophilus oryzae* (Gyllenhal, 1838) (Col: Curculionidae) when presented with their larvae in an artificial laboratory setting (Pérez-Lachaud and Hardy 2001). Terayama (2006) also recorded it from the mountains in Aichi Prefecture on the island of Honshu in Japan, where very little or no coffee is grown or occurs and the coffee berry borer is not known to be present. This raises the question as to what it uses as a host there, or if this record was possibly a misidentification.

### *Prorops obsoleta* Evans, 1977

Known from Trinidad island, Trinidad and Tobago. No recorded hosts.

### *Prorops petila* Evans, 1977

Known from Louisiana, USA; and Guanabara, Brazil. It has been found associated with loblolly pine (*Pinus taeda* L.) (Pinaceae) in Louisiana where it is possibly a parasitoid of *Dendroctonus frontalis* Zimmerman, 1868.

### *Prorops rakan* Terayama, 2006

Known from Aichi Prefecture, Japan. No recorded hosts.

### *Prorops sparsa* Waichert & Azevedo, 2012

Known from Madagascar. No recorded hosts.

In addition to the validly described species above, in an unpublished PhD dissertation Vargas (2017) provided descriptions of three additional species, *Prorops* "sp. 23" from Thailand, *Prorops* "sp. 24" from Vietnam, and *Prorops* "sp. 25" from the United Arab Emirates. No hosts are recorded. The last appears to be the same as the taxon described here as *Prorops umiehu* sp. nov., but we have not been able to examine the UAE specimens to confirm. Mention of these manuscript names and their characters in the key below are not nomenclatural acts (International Commission on Zoological Nomenclature 2012, Art. 8.2).

Both species explored in the present study and described herein were found attacking *Hypothenemus eruditus* Westwood, 1836 (Curculionidae: Scolytinae). This is currently the only known host for both of the species. *Hypothenemus eruditus* is regarded as a supergeneralist, found inhabiting dead wood of a wide variety of tree species over a large taxonomic range, and has even been recorded from fungi (Beaver 1976; Browne 1961; Wood 2007; see Atkinson (2016) for the most comprehensive host list). The type specimens were found boring into the cover of a book, which gave rise to the species name (Westwood 1836). Wood (2007) proposed this species to be the most "widely distributed and abundant" member of Scolytinae in the world. Despite its prevalence, *H. eruditus* rarely achieves high densities and is thought to usually enter only dead wood, and is thus not regarded as a pest species in many environments where it occurs (Kambestad et al. 2017; Tuncer et al. 2017). There are, however, reports of it attacking and damaging a variety of fruit trees including *Malus domestica* Borkh. (apple), *Morus* L. (mulberry), *Ficus carica* L. (fig), *Mangifera indica* L. (mango), *Sesbania sesban* (L.) Merr. (sesban) (Batt 2019, and studies cited therein), *Theobroma cacao* L. (cacao) seedlings (Browne 1961), mature and stored seeds (Wood 1977; Mitchell and Maddox 2010), and stunting the growth of *Dryobalanops aromatica* Gaertn.f. (Malay camphor tree) transplants (Browne 1961), and it thus has in fact been suggested to act as a significant pest of agricultural systems and forest environments in some circumstances. There is known to be wide morphological and genetic variation in this species, even between individuals found in the same plant or gallery, and it is possible that *H. eruditus* is in fact better thought of as a species complex (Kambestad et al. 2017). *Cephalonomia hyalinipennis* Ashmead, 1893 is the only other parasitoid known to attack *H.*

*eruditus* in nature (Bushing 1965, cited within). *Phymastichus coffea* LaSalle, 1990, a parasitoid of the coffee berry borer, was found to attack and develop in *H. eruditus* in a laboratory setting in glass vials (Castillo et al. 2004) but has not been observed to do so in nature. Interestingly, in testing using similar methods but beetles from Hawai'i, *P. coffea* was found not to parasitize *H. eruditus* (Yousuf et al. 2020), possibly because of genetic dissimilarity between the populations of *H. eruditus*.

## Methods

### Species description

Specimens collected from wood and other plant parts were examined and photographed using a Leica MZ16 stereomicroscope or Macropod Pro imaging system. Specimens were also dissected, examined, and photographed using an Olympus CX31 compound microscope. Terminology relating to morphological characters follows Azevedo et al. (2018) and Lanes et al. (2020).

Morphometrics of the head were measured as in Fig. 1, all in full face view. Acronyms in Fig. 1 and descriptions of the measurements are as follows:

**LH** Length of head; longitudinal line even with posterior of vertex to tip of snout.

**LH\S** Length of head not including snout; longitudinal line even with posterior of vertex to base of mandible.

**VOL** Vertex-ocular line; longitudinal line even with posterior of vertex to even with posterior margin of eye.

**LE** Length of eye; posterior margin to anterior margin of compound eye.

**LHAE** Length of head above bottom of eye; longitudinal line even with posterior of vertex to even with anterior margin of compound eye.

**LHBE** Length of head below bottom of eye; longitudinal line even with anterior margin of compound eye to tip of snout.

**WH** Width of head; maximum width of head including eyes.

**WF** Width of frons; minimum distance between compound eyes on frons.

**BEM** Bottom of eye to mandible; longitudinal line from even with anterior margin of compound eye to base of mandible.

**WOT** Width of ocellar triangle; distance between the outer margins of the posterior ocelli.

**OOL** Ocellar-ocular line; shortest distance from margin of posterior ocellus to margin of compound eye.

**AOL** Lateral ocellar line; shortest distance between margin of lateral ocellus and anterior ocellus

**POL** Posterior ocellar line; shortest distance between inner margins of posterior ocelli.

**AOT** Angle between lines joining middle of anterior ocellus and middle of each posterior ocellus.

**LPD** Length of metapectal-propodeal disc; distance along median line from anterior margin of metapectal-propodeal complex to declivity, measured in plane perpendicular to overall surface of disc.

**WPD** Width of metapectal-propodeal disc; greatest transverse distance between lateral marginal carinae or lateral edges of disc, posterior of propodeal spiracles; measured in plane perpendicular to overall surface of disc.

Ratios and measurements were among those typically used in Bethylidae and the genus *Prorops*, with the addition of LHBE : LHAE, which gives a sense of the relative length of the snout and may be useful in the genus *Prorops*. Body length was obtained by adding the length of the head from the apex of the snout to the occipital foramen, the occipital foramen to the anterior of the tegula, the anterior of the tegula to the petiole, and the petiole to the apex of the abdomen, to give the full body length if the body including the head were outstretched. Measurements were made on dried, point mounted specimens. Ranges of coloration reported cover that observed for live individuals and fresh or air dried specimens, and may be outside this range depending on preservation method.

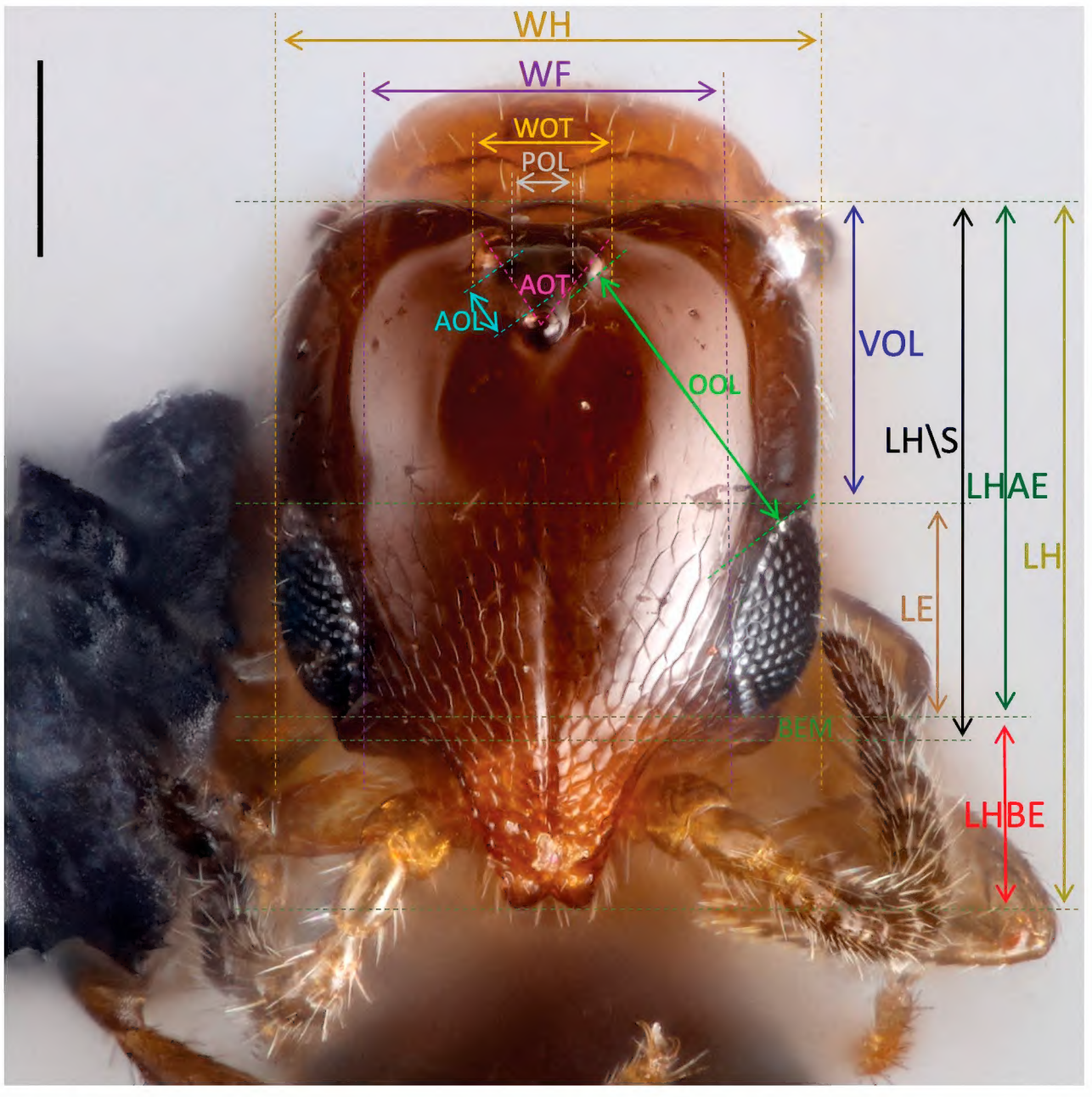


**Figure 1.** *Prorops umiehu* sp. nov. head (paratype) showing morphometric measurements. Acronyms explained in text. Scale bar (upper left): 100 μm.

## Biology and behavior

### Observations of behavior in field-collected plant material

Wood and other plant parts containing Scolytinae were collected in forest, agricultural, and urban environments, and returned to a laboratory for dissection under a microscope.

### Observation chambers in a laboratory setting

Behavior was also observed using "phloem-sandwich" style observation chambers, consisting of thin sheets of plant material compressed between a sheet of plexiglass and a sheet of aluminum, the same apparatus used and described in Honsberger (2024) (Fig. 11a). Such observation chambers were made using either *Trema orientalis* (L.) Blume wood or *Delonix regia* (Boj. ex Hook.) Raf. seed pods. For *T. orientalis*, bark was peeled off branches to the xylem layer and tunnels were cut into the inner surface of the bark with a knife. For *D. regia* seed pods, sections of plant material containing *H. eruditus* tunnels were cut into small pieces and used as they were, or tunnels were cut into uninfested sections of seed pods with a knife. These sections of wood were then placed into the observation chambers, and *H. eruditus* larvae, pupae, and adults, and occasionally other co-occurring beetles collected from *D. regia* pods were placed into the tunnels. Sections of plant material with beetles were sprinkled with debris from the tunnels where the beetles were collected, the plexiglass lid was attached, the boxes were sealed, and female wasps were entered into the boxes through the small holes drilled in the plexiglass.

## Genetic analysis

DNA was extracted from adult wasps using the Qiagen DNeasy Blood and Tissue Kit (Qiagen, Inc., Valencia, Ca, USA), and the CO1 gene was amplified using the primers in Folmer et al. (1994). This was done for two adults of *P. maya* sp. nov., collected from fallen *T. orientalis* branches in the upper reaches of Mānoa Valley, Oʻahu, Hawaiʻi, and described subsequently. The resulting sequences were identical and are reported in GenBank Accession # PP498809.

## Repositories

Specimens are deposited in the following museums:

**UHIM** University of Hawaiʻi Insect Museum, Honolulu, Hawaiʻi, USA
**BPBM** Bernice Pauahi Bishop Museum, Honolulu, Hawaiʻi, USA
**CNC** Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, Ontario, Canada

## Results

***Prorops maya* Honsberger, Lorenzo-Elarco & Magnacca, sp. nov.**
https://zoobank.org/4B7A22E2-5D18-4049-93BA-C4C65F76B6ED
Figs 2, 3

**Diagnosis.** Females can be distinguished from other described *Prorops* spp. by the dark colored head and metasoma contrasting with the orange mesosoma; snout apically bifid and with mesal sulcus; head including snout approximately 1.1 times as long as wide; fore wing with vein 2r-rs+Rs distinct; metapectal-propodeal disc longer than wide in dorsal view, and with lateral carina. Males can be distinguished by the same set of characters except the coloration which is less pronounced than in the females, the head and metasoma brown and the mesosoma lighter yellow-brown.

**Differential diagnosis.** *Prorops maya* females and males can be differentiated from the other species known from Hawai'i, *Prorops umiehu* sp. nov., by the fore wing with vein 2r-rs+Rs distinct (fore wing with 2r-rs+Rs absent in *P. umiehu*); female head only slightly longer than wide (head substantially longer than wide in females of *P. umiehu*); metanotum continuous posterior to mesoscutellum in dorsal view (mesoscutellum covers metanotum medially in *P. umiehu*); mandible more narrow and bidentate (mandible wider and tridentate in *P. umiehu*); clypeus with dorsal and ventral margins more acutely rounded (clypeus dorsal margin more broadly rounded and ventral margin less curved in *P. umiehu*); metapectal-propodeal complex with lateral marginal carina (lateral marginal carina weaker or absent in *P. umiehu*); females by the more distinct coloration, with the mesosoma orange and the head and metasoma dark brown (head and mesosoma of similar reddish-brown color, sometimes mesosoma lighter but only slightly, in *P. umiehu* females).

**Female** (Figs 2a–d, 3). ***Length range*:** 1.10–1.23 mm (n = 6), Holotype 1.23 mm

***Head*** (Figs 2b, c, 3c, e). Frons, gena, vertex, and occiput dark brown and shiny with sparse setae. Very anterior of head, including snout, basal antennomeres, mandible, clypeus, and mouthparts lighter in color, often orange, of similar color to mesosoma. Frons and gena with lightly reticulate texture, density of reticulations increasing towards snout, snout itself with bumpy texture. Compound eye with short, sparse setae between ommatidia. Vertex incurved. Head with sides more or less parallel and only slightly outcurved, eye projecting slightly so widest part of head is across eyes. Snout bifid apically, but indistinctly in face view, ending in two lobes apically curved dorsally to form two small teeth; with dorsal median groove extending from where lobes meet to even with anterior of compound eye, sometimes continuing more weakly to approximately even with middle of eye. Torulus located ventral to lateral margins of snout at approximately half its length, visible in dorsal view. Clypeus in anterior view extending laterally past torulus, tapers laterad; medially with dorsal margin somewhat acutely arched against snout and torulus, ventral margin strongly incurved; overall appearing as handlebar mustache turned dorsad at its lateral corners. Antenna with scape curved ventrally and widened apically, its apical surface forming cavity. Pedicel slightly rounded subquadrate, with somewhat nodose basal section connected to dorsal portion of cavity at apex of scape.

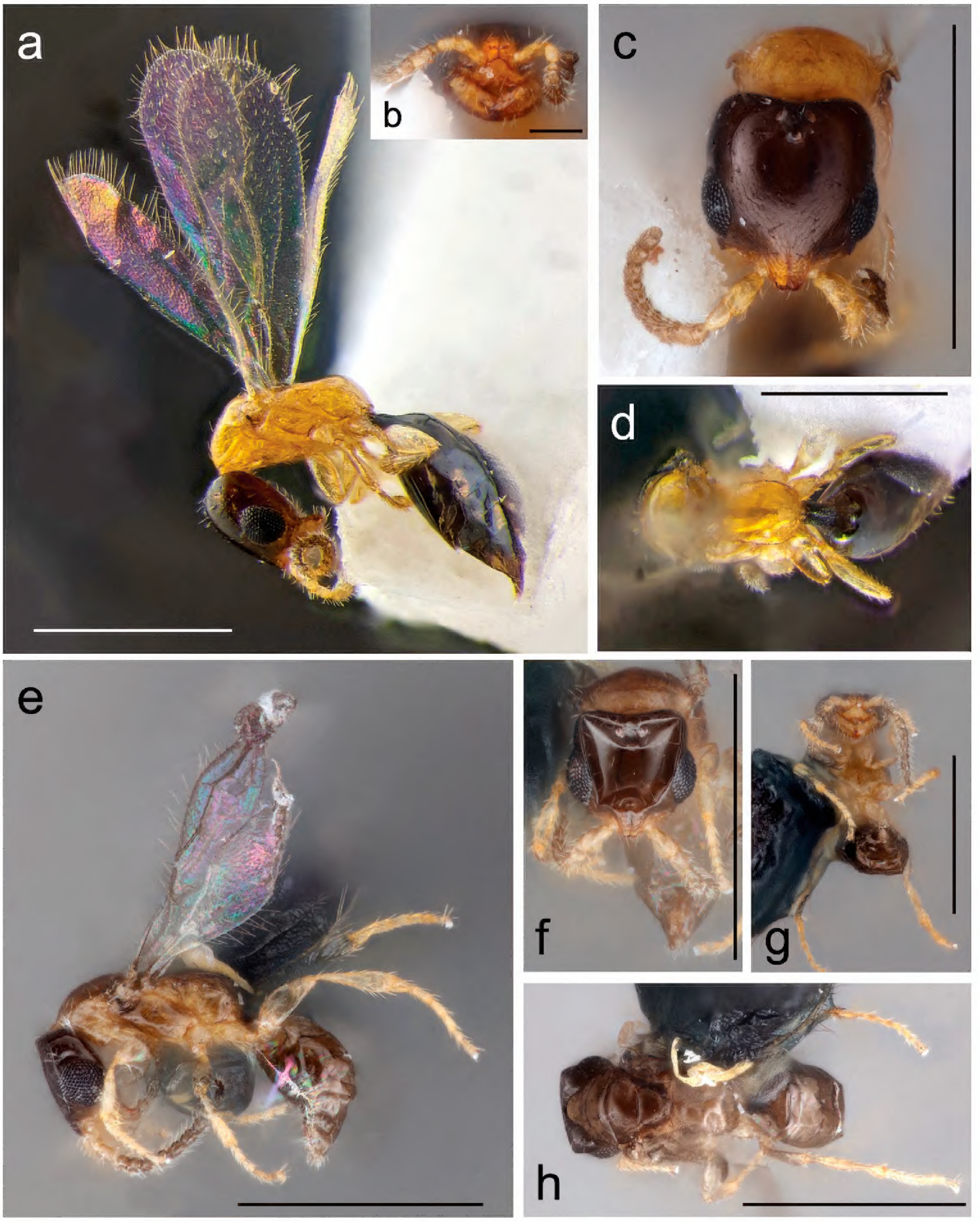


**Figure 2.** *Prorops maya* sp. nov. holotype ♀ (**a–d**) and allotype ♂ (**e–h**) **a, e** side view **b, g** anterior view of head **c, f** head **d, h** dorsal view. Scale bars: 500 μm (**a, c–h**); 100 μm (**b**).

Ten flagellomeres, 1st smallest and cone shaped, 2nd through 9th shaped like apically truncated spheres, and similar in size, shape, and structure. Terminal flagellomere ovate. Setae of similar length and density on all flagellomeres, less dense on scape and pedicel. Antenna yellow-orange to orange at least basally, apical flagellomeres darker. Mandible with two apical teeth; ventral tooth longer, two thick setae on mandible just dorsad of

teeth. Anterior region of head, including snout, clypeus, and mandible, distinctly more densely setose than rest of head. ***Morphometrics*** (range, n = 3 for all measurements): LH : WH = 1.06–1.11; LH : LE = 2.65–2.78; LH : VOL = 2.51–2.58; LHBE : LHAE = 0.29–0.34; VOL : LE = 1.05–1.08; WF : LE = 1.60–1.70; LE : BEM = 5.70–7.42; WOT : OOL = 0.46–0.50; POL : AOL = 1.13–1.28; AOT = 70°–75°; LH\S : WH = 0.89–0.93. Antennal ratio approximately Scape : Pedicel : F1 : F2 : F3 : F4 : F5 : F6 : F7 : F8 : F9 : F10 = 3.3 : 2.1: 1.0 : 1.3 : 1.3 : 1.4 : 1.4 : 1.5 : 1.6 : 1.6 : 1.6 : 2.4.

***Mesosoma*** (Figs 2a, d, 3d). Mesosoma bright orange, contrasting with brown head and metasoma. Pronotum shiny and with light reticulate texture posterior to pronotal flange; pronotal flange conspicuous, shiny with faintly coriaceous texture; other thoracic nota and metapectal-propodeal complex smooth and shiny with only very light reticulate texture, difficult to see except under high magnification and with the right lighting, anteromesoscutum and posterior region of metapectal-propodeal disc especially smooth and glassy. Pronotum with sparse setae, longer setae at posterior margin. Anteromesoscutum with scattered short mesal pointing setae; mesoscutellum with pair of short setae on its lateral margin approximately even with posterior margin of axillae, another pair of longer mesally pointing setae at its posterior; axillae with sparse, short setae; tegula with few setae, denser than on surrounding sclerites; metanotum with pair of setae near its posterior margin, approximately in line with lateral margin of mesoscutellum; metapectal-propodeal disc without setae, declivity with few setae just mesal of lateral carina. Transscutal suture such that posterior margin of anteromesoscutum is slightly outcurved. Anterior boundary of anteromesoscutum somewhat visible under translucent pronotum. Mesosoma relatively flat along dorsomedian line. Notaulus somewhat visible as dark streak but does not manifest on cuticle surface. Parapsidal signum present but very light. Metanotum continuous and visible posterior to mesoscutellum, thin and slightly elevated medially, wider laterally. Length of mesoscutellum approximately 2.5 times length of metanotum on medial line. Mesopleuron projects from side of mesosoma, flattened subcylindrical in shape, though tapering slightly near connection with mesocoxa, and with few setae only on its ventral side. Mesopleural pit somewhat centrally located. Metapectal-propodeal disc approximately 1.2 times as long as wide; flat medially, vaguely outcurved towards lateral edges mesal of lateral marginal carina; lateral marginal carina often distinct but somewhat weak in some individuals, becoming less distinct on declivity before reaching petiole; shape of declivity subtriangular when viewed perpendicular to its surface. Lateral surface of metapectal-propodeal complex flat or slightly convex, inclined past vertical.

***Legs*** (Fig. 3f–h). Legs of similar color to rest of mesosoma, sometimes a bit lighter. All tibiae with scythe shaped apical spur with comb-like setae on inner edge. Mesotibia with apical spines more numerous and stronger than in pro- and metatibiae, and with additional row of strong spines over its length on side opposite tibial spur; pro- and metatibia lacking this row of spines. First tarsomere longest in each leg, most notably so in pro- and metalegs where it is only slightly shorter than 2$^{nd}$ through 4$^{th}$ tarsomeres combined. 2$^{nd}$ through 4$^{th}$ tarsomeres subequal in length in proleg, sequentially decrease in length in meso- and metaleg. Length of 5$^{th}$ tarsomere not including claw subequal to combined length of 2$^{nd}$ and 3$^{rd}$ tarsomeres in proleg, and subequal to 2$^{nd}$ segment alone in meso- and metalegs.

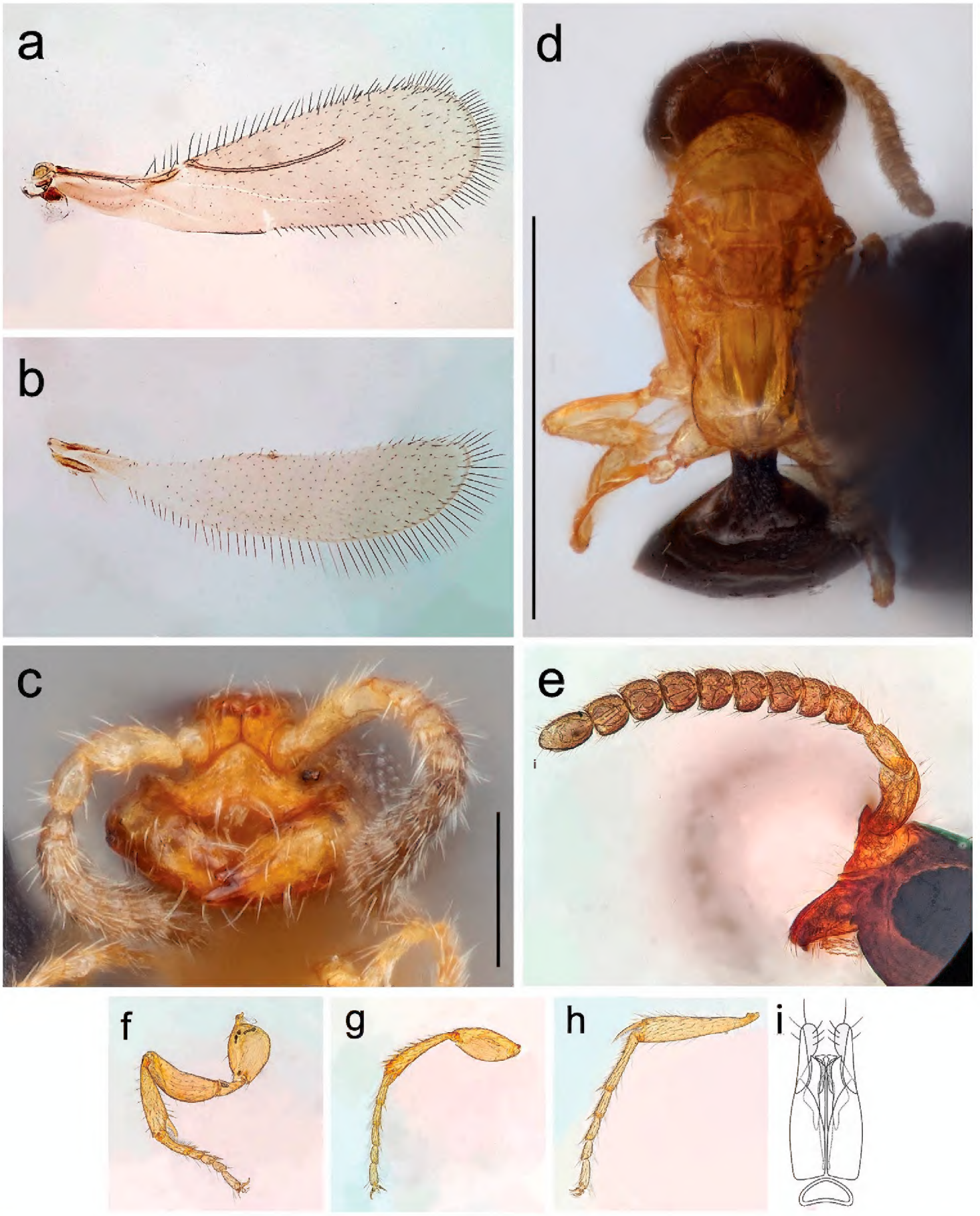


**Figure 3.** *Prorops maya* sp. nov. **a** fore wing ♀ **b** hind wing ♀ **c** anterior view of head ♀ (paratype) **d** dorsal view ♀ (paratype, wings removed) **e** antenna ♀ **f** proleg ♀ **g** mesoleg ♀ **h** metaleg ♀ **i** male genitalia, ventral view. Scale bars: 100 μm (**c**); 500 μm (**d**).

***Fore wing*** (Fig. 3a). Sc+R vein, prestigmal abcissa of radial 1, pterostigma, and 2r-rs+Rs vein strong. Rs+M, M+Cu, and A veins lightly indicated. Sc+R vein with three setae. 2r-rs+Rs vein extending from pterostigma to approximately 0.7× full length of wing. Prestigmal abcissa of radial 1 inset from wing margin, pterostigma borders margin.

Prestigmal flexion line present as hyaline stripe separating prestigmal abcissa of radial 1 and pterostigma; thickness of hyaline stripe and shape of prestigmal abcissa of radial 1 and pterostigma somewhat variable among individuals, though prestigmal abcissa of radial 1 usually longer than pterostigma and neither wider than approximately twice width of basal part of 2r-rs+Rs vein. Wing membrane subhyaline, with the following additional flexion lines visible as hyaline stripes. Cubital flexion line emerges just posterior to where indications of M+Cu and A veins meet, bounded by small setae and pointing towards middle of retinaculum, fading before reaching wing margin. Longer, somewhat wavy median flexion line emerges just posterior of prestigmal abcissa of radial 1, generally pointing apicad of trailing edge of wing and reaching approximately even with end of 2r-rs+Rs vein, also marked by trail of short setae. Wing membrane posterior and basal to median flexion line with few setae other than those bounding cubital flexion line and indications of Rs+M, M+Cu, and A veins in basal region of wing. Small hyaline spot projects into wing membrane on its posterior margin just apical of retinaculum. Marginal setae present from prestigmal abcissa of radial 1 around to apex of retinaculum. ***Hind wing*** (Fig. 3b). Wing membrane subhyaline with short setae of approximately equal length and density over its surface. Marginal setae short on leading edge, longest around apical margin and on apical half of trailing edge where their length is about half maximum width of wing, gradually decreasing basad towards basal trailing margin. Leading edge with slight projection culminating in dark spot with three hamuli at about half wing length.

***Metasoma*** (Figs 2a, d, 3d). Petiole and metasoma dark brown to black, in distinct contrast with orange mesosoma. First tergite constricted anteriorly to form distinct petiole, segment as a whole somewhat wider than long; constricted petiolar region of subequal length and width, with fine bumpy texture and shallow median dorsal groove extending its length. Remainder of metasoma shiny dark brown to black with smooth texture and sparse setae over most of its length. Very few setae present dorsally in anterior half; setae steadily increase in density in posterior third both dorsally and laterally, ring of setae present at apex of metasoma where sting emerges. In dorsal view, petiole and 2nd metasomal segment subequal in length on median line, 3rd and 4th also subequal but shorter than 1st and 2nd. Metasoma widest near posterior margin of 4th segment. Sting often visible projecting slightly from apex of abdomen in dried or alcohol preserved specimens.

**Male** (Fig. 2e–h). ***Length range*:** 0.75–0.97 mm (n = 2), Allotype 0.97 mm. As in female but with the following differences. Coloration dull, head and metasoma brown, mesosoma yellowish brown. 2nd through 9th antennal flagellomeres of more cylindrical shape, longer than wide, and antenna overall longer than in female relative to body size. Morphometrics of head similar to that of female, but with eye larger and more bulging relative to face than female; exact ratios could not be obtained because faces of the two known specimens were somewhat collapsed. ***Genitalia*:** See Fig. 3i. Small relative to body size. Genital capsule narrow, gonostipites and harpes combined about twice as long as wide; harpe elongate, about 2/3 as long as gonostipes, broadly rounded distally. Penis valvae much shorter than volsella, mostly concealed in ventral view.

**Materials examined.** ***Holotype*** (Fig. 2a–d): ♀; Hawaiian Islands, Oʻahu, Mānoa Valley; 21.3288°N, 157.7930°W, 154 m; 12.ii.2020; ex *Hypothenemus eruditus* tunnel in *Trema orientalis* branch; D. Honsberger (UHIM).

***Allotype*** (Fig. 2e–h): ♂; same data as holotype; (UHIM).

***Paratypes*:** 7 ♀, 1 ♂; all with same data as holotype (2 ♀ UHIM, 1 individual with wings removed; 3 ♀, 1 ♂ BPBM; 2 ♀ CNC).

**Etymology.** This beautiful wasp is named after Maya Honsberger, a wonderful and beautiful human being. It has also been elusive for us to find, all individuals found on only one occasion, as with Maya, for whom it is also rare to find as wonderful a wife as her. The name is to be treated as a noun in apposition.

For the Hawaiian common name, maiʻapala (lit., *ripe banana*) was selected. Maiʻa (general term for banana) is similar in sound and spelling to the species name *maya* and also one of the favorite foods of Maya Honsberger, combined with the similarity of the yellow and brown coloration of the wasp to a ripe (pala) banana.

**Known distribution.** This species is known from the island of Oʻahu in Hawaiʻi, where it is likely adventive. Based on its limited abundance and distribution, it is probably a recent arrival.

**Known hosts.** *Hypothenemus eruditus* (Coleoptera: Scolytinae); see Biology section.

***Prorops umiehu*** **Honsberger, Lorenzo-Elarco & Magnacca, sp. nov.**
https://zoobank.org/31D3C969-F035-4AE8-A31A-A5401A8B800F
Figs 4, 5

**Diagnosis.** Females can be distinguished from other described *Prorops* spp. by the combination of: head and mesosoma orangish-brown to reddish-brown; fore wing without vein 2r-rs+Rs; snout bifid and with mesal sulcus; head including snout approximately 1.3 times as long as wide; metapectal-propodeal disc approximately 1.2 times longer than wide in dorsal view, and without distinct lateral carina. Males can be distinguished by the same set of characters as the females except for coloration and morphometrics of the head: body darker in color, brownish; head including snout approximately 1.1 times as long as wide.

**Differential diagnosis.** *Prorops umiehu* can be differentiated from *Prorops maya* by lack of vein 2r-rs+Rs in the fore wing (2r-rs+Rs distinct in *P. maya*); metapectal-propodeal complex and mesoscutellum overlapping medially, dividing metanotum in dorsal view (metanotum continuously visible posterior to mesoscutellum in *P. maya*); female head 1.3 times as long as wide, male head 1.1 times as long as wide (head 1.1 times as long as wide in both sexes of *P. maya*); mandible wide and tridentate, though dorsal tooth small and inconspicuous (mandible more narrow and bidentate in *P. maya*); clypeus with anterior margin broadly rounded, posterior margin slightly emarginate (anterior margin acutely rounded, posterior margin sinusoidal in *P. maya*); metapectal-propodeal complex without distinct lateral marginal carina (lateral marginal carina more distinctly conspicuous in *P. maya*); female with head and mesosoma of similar orange-red-brown color (dark brown head and metasoma contrasting with orange mesosoma in *P. maya* female).

**Female** (Figs 1, 4a–d, 5). ***Length range*:** 1.18–1.41 mm (n = 11); Holotype: 1.38 mm. ***Head*** (Figs 1, 4a–c, 5c, e). Face, gena, vertex, and occiput orange to red-brown

**Figure 4.** *Prorops umiehu* sp. nov. holotype ♀ (**a–d**) and allotype ♂ (**e–g**) **a, e** side view **b, f** head **c, g** anterior view of head **d** dorsal view. Scale bars: 500 μm (**a, b, d, e**); 250 μm (**c, f, g**).

in color. Snout slightly lighter orange-brown, antenna yellow-brown basally, fading to brown apically. Frons and gena with lightly reticulate texture, density of reticulations increasing towards snout, snout itself with bumpy texture. Compound eye with short, sparse setae between ommatidia. Vertex incurved medially. Head with sides more or

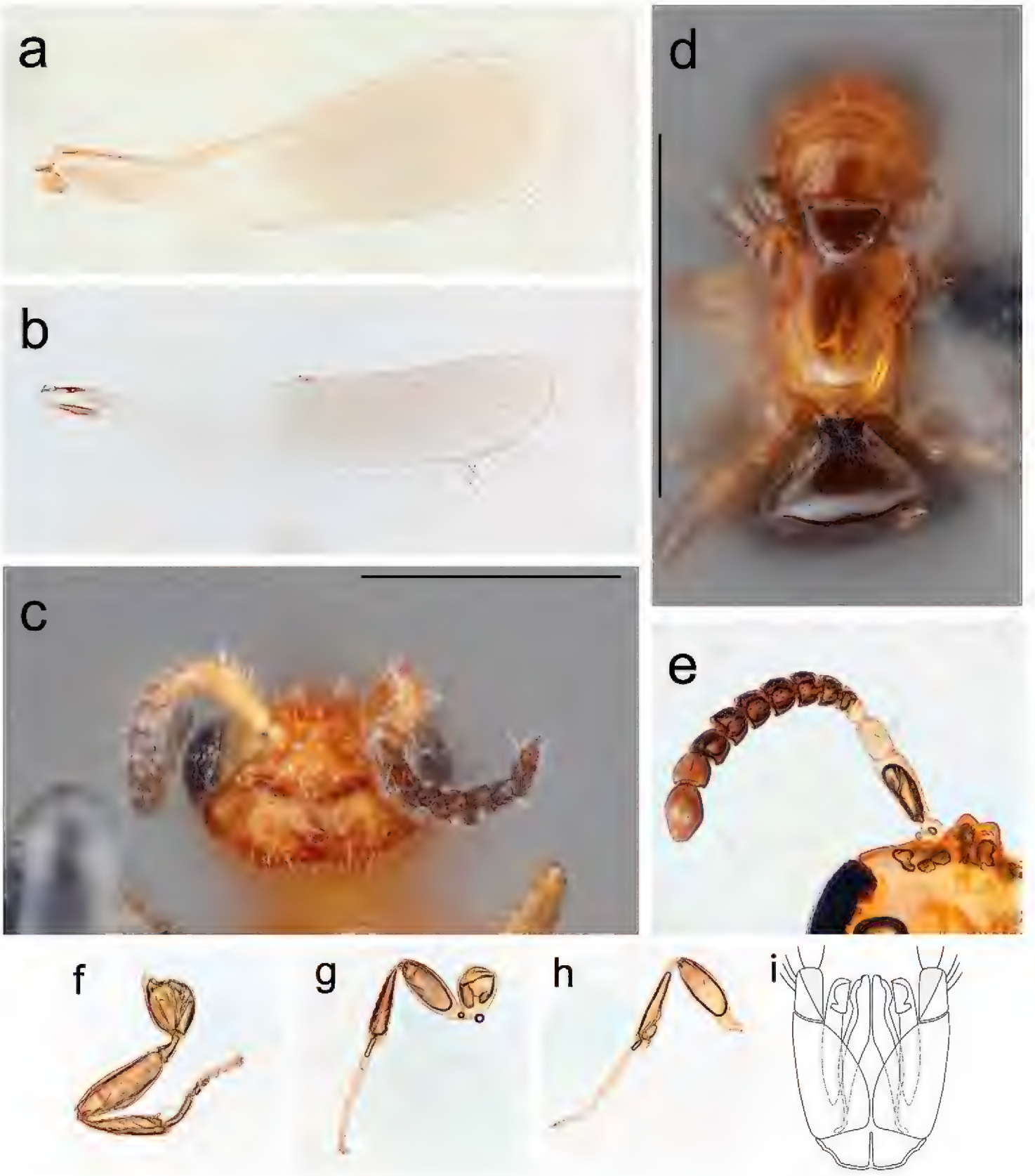


**Figure 5.** *Prorops umiehu* sp. nov. **a** fore wing ♀ **b** hind wing ♀ **c** anterior view of head ♀ (paratype) **d** dorsal view ♀ (paratype) **e** antenna ♀ **f** proleg ♀ **g** mesoleg ♀ **h** metaleg ♀ **i** male genitalia, ventral view. Scale bars: 250 μm (**c**); 500 μm (**d**).

less parallel and only slightly outcurved, eye protruding slightly so widest part of head is across eyes and about half-way along VOL. Snout clearly bifid apically, ending in two distinct lobes apically curved dorsally to form two small teeth, and with dorsal median groove extending from where lobes meet to approximately even with middle of eye. Torulus located ventral to lateral margins of snout at approximately half its length, visible in dorsal view. Clypeus in anterior view extending laterally past torulus, tapers

laterad; medially with dorsal margin broadly arched against snout and torulus, ventral margin shallowly incurved; overall appearing as handlebar mustache not, or only slightly, turned dorsad at its lateral corners. Antenna with scape curved ventrally and widened apically, apical surface forming cavity; pedicel subovate. Ten flagellomeres, 1st smallest and cone shaped, 2nd through 9th shaped like apically truncated spheres, and similar in size, shape, and structure. Terminal flagellomere ovate. Setae of similar length and density on all flagellomeres, less dense on scape and pedicel. Mandible wide, ventral margin thickened with blunt ventral knob at about half its length; apically tridentate, ventral tooth largest, middle tooth smaller, dorsal tooth small and inconspicuous. Anterior region of head, including snout, clypeus, and mandible, distinctly more densely setose than rest of head. ***Morphometrics*** (range, n = 7 for all measurements): LH : WH = 1.24–1.31; LH : LE = 3.26–3.64; LH : VOL = 2.19–2.34; LHBE : LHAE = 0.35–0.38; VOL : LE = 1.41–1.66; WF : LE = 1.70–1.87; LE : BEM = 5.71–7.30; WOT : OOL = 0.40–0.45; POL : AOL = 1.10–1.54; AOT = 66°–75°; LH\S : WH = 0.97–1.03. Antennal ratio approximately Scape : Pedicel : F1 : F2 : F3 : F4 : F5 : F6 : F7 : F8 : F9 : F10 = 4.0 : 2.6 : 1.0 : 0.9 : 1.2 : 1.2 : 1.4 : 1.4 : 1.5 : 1.6 : 1.6 : 2.9.

***Mesosoma*** (Figs 4a, d, 5d). Pronotum and metapectal-propodeal complex yellow to reddish-brown; mesothorax slightly darker in some individuals; legs apical of femora yellow-brown. Nota shiny with very light reticulate texture, difficult to see except under high magnification with the right lighting. Texture on dorsal surfaces slightly strongest on pronotal flange and metapectal-propodeal disc. Pronotal flange conspicuous; pronotum with sparse setae, longer setae at posterior margin. Anteromesoscutum with scattered short setae; mesoscutellum with pair of short setae on its lateral margin approximately even with posterior of axillae, another pair of longer mesally pointing setae at its posterior; tegula with few setae, denser than on surrounding sclerites; metapectal-propodeal disc without setae, declivity with few setae just mesal of transition to lateral surface of metapectal-propodeal complex. Transscutal suture such that posterior margin of anteromesoscutum is straight mesal of axillae. Anterior margin of anteromesoscutum somewhat visible under translucent pronotum. Mesosoma relatively flat along dorsomedian line. Neither notaulus nor parapsidal signum manifest on cuticle surface. Mesocutellum reaches metapectal-propodeal complex medially, metanotum very thin or not visible medially in dorsal view, distinct laterally. Mesopleuron projects from side of mesosoma, flattened subcylindrical in shape, and with few setae only on its ventral side. Mesopleural pit somewhat centrally located. Metapectal-propodeal disc approximately 1.25 times as long as wide; lateral marginal carina indistinct or absent, transition from disc to lateral surface rounded, though cuticle may appear thickened in dorsal view at this transition; disc somewhat outcurved transversely. Declivity when viewed perpendicular to its surface has vaguely subtriangular raised region, but appears overall subrectangular: posterior margin of metapectal-propodeal complex straight except for small bump above petiolar foramen. Lateral surface of metapectal-propodeal complex flat or slightly convex.

***Legs*** (Fig. 5f–h). All tibiae with scythe shaped apical spur with comb-like setae on inner edge. Mesotibia with apical spines more numerous and stronger than in pro- and

metatibiae, and with additional row of strong spines over its length on side opposite tibial spur; pro- and metatibiae lacking this row of spines. First tarsomere longest in each leg, most notably so in pro- and metaleg where it is subequal to 2nd through 4th tarsomeres combined. 2nd through 4th tarsomeres subequal in length in proleg, and sequentially decrease in length in meso- and metalegs. Length of 5th tarsomere not including claw subequal to combined length of 2nd and 3rd tarsomeres in proleg, and subequal to 2nd segment alone in meso- and metalegs.

***Fore wing*** (Fig. 5a). Sc+R vein, prestigmal abcissa of radial 1, and pterostigma present; 2r-rs+Rs absent, reduced to fold. Rs+M, M+Cu, and A veins lightly indicated. Sc+R vein with 1–3 setae. Prestigmal abcissa of radial 1 slightly inset from wing margin, pterostigma borders margin. Prestigmal flexion line present as hyaline stripe that separates prestigmal abcissa of radial 1 and pterostigma; thickness of this hyaline stripe and shape and size of prestigmal abcissa of radial 1 and pterostigma somewhat variable among individuals, though prestigmal abcissa of radial 1 and pterostigma typically subequal in size. Wing membrane overall subhyaline, slightly infuscate basal of prestigmal abcissa of radial 1 and apical of imaginary line between pterostigma and apex of retinaculum. Cubital and median flexion lines not visibly present; small hyaline spot projects into wing membrane on posterior margin at apex of retinaculum. Marginal setae present from prestigmal abcissa of radial 1 around wing apex, abruptly ending at beginning of straight trailing margin of wing. ***Hind wing*** (Fig. 5b). Wing membrane subhyaline, slightly infuscate apical of hamuli. Marginal setae absent on leading edge, present around apical margin and on trailing edge where length is about half maximum width of wing. Leading edge with slight projection culminating in dark spot with three hamuli at about half wing length.

***Metasoma*** (Figs 4a, b, 5d). Petiole and gaster dark brown to black, distinctly darker than orangish-brown mesosoma. First tergite constricted anteriorly to form distinct petiole, segment as a whole somewhat wider than long; constricted petiolar region of subequal length and width, with fine bumpy texture and shallow median dorsal groove extending its length. Remainder of metasoma shiny dark brown to black with smooth texture, each segment dorsally with sparse setae in a somewhat transverse row, these setae increasing slightly in length on posterior segments, last segment before sting with many setae on dorsal and lateral surfaces. In dorsal view, 1st and 2nd gastral segments subequal in length on median line, 3rd and 4th also subequal but shorter than 1st and 2nd. Metasoma widest at approximately 4th segment. Sting often visible projecting slightly from apex of abdomen in dried or alcohol preserved specimens.

**Male** (Figs 4e–g, 5i). ***Length range*:** 0.87–1.38 mm (n = 3); Allotype: 1.38 mm

As in female but with the following differences: Head more square than in female, length to width ratio approximately 1.1; eye larger and more bulging; ocelli more widely placed; vertex only weakly concave; 2nd through 9th antennal flagellomeres longer and more cylindrical; coloration typically darker with head and metasoma brown, mesosoma slightly lighter brown. ***Genitalia*:** See Fig. 5i. Small relative to body size. Genital capsule broad, gonostipites and harpes combined only slightly longer than wide; harpe short, quadrate, truncate distally, shallowly concave medially. Penis valvae equal to or slightly exceeding volsella, distinct in ventral view. ***Morphometrics*** (range, n = 3 for all measurements):LH : WH = 1.07–1.12; LH : LE = 2.48–2.63; LH : VOL = 2.71–3.11;

LHBE :LHAE = 0.33–0.38; VOL : LE = 0.80–0.96; WF : LE = 1.42–1.58; LE : BEM = 6.34–7.72; WOT : OOL = 0.63–0.74; POL : AOL = 1.35–1.68; AOT = 75°–82°; LH\S : WH = 0.87–0.88

**Materials examined.** ***Holotype*** (Fig. 4a–d): ♀; Hawaiian Islands, Oʻahu, Kahana Bay; 21.5573°N, 157.8781°W, 15 m; 27.viii.2021; ex *Trema orientalis* branches; D. Honsberger (UHIM).

***Allotype*** (Figs 4e–g, 9): ♂; Hawaiian Islands, Oʻahu, Mānoa Valley; 21.3288°N, 157.7930°W, 154 m; 12.ii.2020; ex *H. eruditus* tunnel in *T. orientalis* branch; D. Honsberger (UHIM).

***Paratypes*:** 18 ♀, 5 ♂. Hawaiian Islands, Oʻahu, Kahana Bay; 21.5573°N, 157.8781°W, 15 m; 27.viii.2021; ex *Trema orientalis* branches; D. Honsberger (1 ♀, 1 ♂ BPBM) • Hawaiian Islands, Oʻahu, Mānoa; 21.3009°N, 157.8196°W, 39 m; 20.v.2021; ex *Delonix regia* seed pod; D. Honsberger (1 ♀ BPBM) • same data as previous except 13.iv.2021 (1 ♀ UHIM; 1 ♀ BPBM; 1 ♀ CNC) • Hawaiian Islands, Oʻahu, Mānoa; 21.3009°N, 157.8196°W, 39 m; 23.iv.2021; reared from *Hypothenemus eruditus* adult in *Delonix regia* seed pod; D. Honsberger (1 ♀ CNC) • Hawaiian Islands, Oʻahu, Waimānalo; 21.3341°N, 157.7113°W, 28 m; 19.ii.2021; reared from *Hypothenemus seriatus* adult in *Macadamia integrifolia* husk; D. Honsberger (1 ♀ UHIM) • Hawaiian Islands, Oʻahu, Wahiawā; 21.5151°N, 158.0423°W, 296 m; 11.i.2020; ex *Hypothenemus eruditus* tunnel in *Spathodea campanulata* branch; D. Honsberger (1 ♂ CNC) • Hawaiian Islands, Oʻahu, Wahiawā; 21.5143°N, 158.0419°W, 301 m; 1.iii.2019; ex *Spathodea campanulata* branches; D. Honsberger (1 ♀ CNC) • Hawaiian Islands, Oʻahu, Pearl Harbor; vi.1954 (1 ♀ BPBM) • Hawaiian Islands, Oʻahu, Waipiʻo; ix.1957; light trap; J.W. Beardsley (1 ♂ BPBM) • Hawaiian Islands, Oʻahu, Waipiʻo; ii.1960; light trap; J.W. Beardsley (1 ♀ BPBM) • Hawaiian Islands, Oʻahu, Pearl Harbor, West Loch, el. 3 ft; 13–24. vi.1998; yellow sticky board trap; W.D. Perreira (2 ♀ BPBM) • Hawaiian Islands, Molokaʻi, Kamalō Bridge, 3 ft.; 19.viii–2.ix.1994; yellow sticky board trap; W.D. Perreira (1 ♀ BPBM) • Hawaiian Islands, Molokaʻi, Kualapuʻu in coffee field, el. 750 ft.; 27.x–10.xi.1995; yellow sticky board trap; J.W. Beardsley and W.D. Perreira (1 ♀ BPBM) • Hawaiian Islands, Maui, Kahului Airport; 4.x.1999; Malaise trap site #1, wet spot nr. bike path, nr. water amongst kiawe & palm trees; F.G. Howarth, D.J. Preston, & J. Dockall (1 ♀ BPBM) • Hawaiian Islands, Maui, Kahului Airport; 20°54'22"N, 156°25'42"W; 3–16.xii.1999; Malaise trap site #2; F.G. Howarth, D.J. Preston, F. Starr, & K. Martz (1 ♂ BPBM) • Hawaiian Islands, Maui, Kahului Airport; 20°54'22"N, 156°25'56"W; 1.ii.2000; Malaise trap site #1; F.G. Howarth, D.J. Preston, J.E. Dockall, F. Starr, & K. Martz (1 ♂ BPBM) • Hawaiian Islands, Hawaiʻi, Honomalino; iv.1987; carob fruits; HY 87–14; G. Shaner (3 ♀ BPBM) • Hawaiian Islands, Hawaiʻi, MacFarms; 9.iii.1995 (2 ♀ BPBM).

**Etymology.** The species name is Hawaiian, ʻumiʻehu (lit., *blonde mustache*). When the head is viewed anteriorly (Fig. 5c), the clypeus appears as a blonde (ʻehu) handlebar mustache (ʻumiʻumi) between its snout and mouth. This small, cryptoparasitic wasp also appears like a mist (ʻehu) in the environment, often faintly perceptible and then evaporates from view. The name is to be treated as a noun in apposition.

**Known distribution.** This species is known from the islands of O'ahu, Moloka'i, Maui, and Hawai'i in the Hawaiian Islands, where it is likely adventive, and from the United Arab Emirates near Al Ajban, Emirate of Abu Dhabi (Vargas 2017). It has long been present in the islands, with the earliest Hawai'i specimen dating back to 1954. This suggests it may have arrived from the southwest Pacific during World War II or shortly afterward.

**Known hosts.** *Hypothenemus eruditus* and *Hypothenemus seriatus* (Coleoptera: Scolytinae); see Biology section.

## Key to the known world species of *Prorops*

Note that males of *P. rakan*, *P. mandibularis*, *P.* "sp. 23", and *P.* "sp. 24" are currently unknown.

1 Fore wing without vein 2r-rs+Rs, or 2r-rs+Rs vein very faint, reduced to fold ..... **2**

– Fore wing with distinct vein 2r-rs+Rs emanating from pterostigma ..... **4**

2 Snout with median groove but not clearly bifid, instead rounded or trifid apically; notauli present ..... ***P. obsoleta*** (♀♂)

– Snout clearly bifid apically (ends in two distinct lobes); notauli absent ..... **3**

3 LH subequal to WH; metapectal-propodeal disc wider than long, LPD:WPD ≈ 0.9 (both sexes); AND if female, vertex slightly incurved in face view; if male, vertex nearly straight in face view ..... ***P. impotens*** (♀♂)

– Metapectal-propodeal disc longer than wide, LPD:WPD ≈ 1.25; vertex distinctly incurved in face view (both sexes); AND if female, LH:WH ≈ 1.3; if male, LH:WH ≈ 1.1 ..... ***P. umiehu*** (♀♂)

4 Snout divided into two widely separated arms not contiguous basally or apically ..... ***P. sparsa*** (♀♂)

– Snout divided or with median groove, but contiguous at least basally ..... **5**

5 Snout with median groove but rounded apically, not clearly bifid ..... **6**

– Snout clearly bifid apically (ends in two distinct lobes ..... **7**

6 LH:WH ≈ 1.6, and LH\S also distinctly greater than WH; LHAE:LHBE ≈ 2.9; mandible tridentate; lengths of first four antennomeres with ratio of 10:3:1:2; head with vertex somewhat straight ..... ***P. petila*** (♀♂)

– LH:WH ≈ 1.3, and LH\S subequal to WH; snout long, LHAE:LHBE ≈ 1.3; mandible bidentate; first four antennomeres in ratio of 3.5:1.6:1.1:1.0; head with vertex incurved medially ..... ***P. mandibularis*** (♀)

7 LH:WH ≈ 1.4, first four antennomeres in ratio of 5:2:1:1; mandible tridentate ..... ***P. rakan*** (♀)

– LH subequal to WH ..... **8**

8 In females, mesosoma, mandible, snout, and basal region of antenna bright orange to reddish brown, in distinct contrast with metasoma and remainder of head almost black; in males, head and metasoma brown, mesosoma light

brown. In both sexes, LPD distinctly greater than WPD, disc shiny with lateral carina, declivity also smooth and shiny with lateral carina at least anteriorly; mesonotum with only a few setae, usually just 2 on each side of median line of mesoscutellum; metanotum visible as continuous narrow band posterior to mesoscutellum in dorsal view; LH:WH ≈ 1.1; LHAE:LBHE ≈ 3–3.5 ..... ***P. maya*** (♀♂)

– Coloration entirely dark brown to black; WPD subequal to or greater than LPD, disc without lateral marginal carina; mesonotum with few to many setae on both anteromesoscutum and mesoscutellum; mesoscutellum covers metanotum medially ..... **9**

9 Head widest across eyes, narrowing between eye posterior margin and vertex; WPD slightly greater than 1.5 times LPD; LH:LE ≈ 2.4; LHAE:LHBE ≈ 2.5; mesonotum setose, including medially; mesoscutum with slightly rough texture, metapectal-propodeal disc smooth and glassy; head with vertex strongly incurved..... ***P.* "sp. 23" [of Vargas (2017)]** (♀)

– Width of head just anterior to vertex subequal to or slightly greater than width across eyes; WPD distinctly less than 1.5 times LPD; LH:LE > 2.5; LHAE:LHBE < 2.0..... **10**

10 Vertex only somewhat incurved, such that anterior ocellus slightly posterior to top of compound eye in full face view; WH:LE ≈ 2.5; LH:LE ≈ 2.9; LHAE:LHBE ≈ 1.9; WH:LHBE ≈ 1.4; metapectal-propodeal disc only slightly wider than long, WPD:LPD ≈ 1.1, disc with rough texture; mesoscutum and scutellum setose, including medially ..... ***P. nasuta*** (♀♂)

– Vertex strongly incurved, such that anterior ocellus slightly anterior to top of compound eye in full face view; eyes smaller, so that WH:LE ≈ 3.3; LH:LE ≈ 2.4; LHAE:LHBE ≈ 1.3; WH:LHBE ≈ 1.7; metapectal-propodeal disc substantially wider than long, WPD:LPD ≈ 1.3, disc smooth and glassy; mesoscutum less setose, with few or no setae medially on mesoscutum ..... ..... ***P.* "sp. 24" [of Vargas (2017)]** (♀)

## Biology

### Known hosts

*Prorops maya* has been found parasitizing *H. eruditus* adults in *Trema orientalis* (gunpowder tree) branches in Mānoa Valley at the foot of the Koʻolau Mountains on Oʻahu island (21.3288°N, 157.7930°W, 154 m) (Fig. 6).

*Prorops umiehu* has been found parasitizing *H. eruditus* in *T. orientalis* branches and *D. regia* seed pods in Mānoa, Oʻahu island, and *Hypothenemus seriatus* in macadamia nut husks in Waimānalo, Oʻahu (Figs 6, 7). It has been found emerging from *Spathodea campanulata* P.Beauv (African tulip) branches near Wahiawā, Oʻahu and *Ceratonia siliqua* L. (carob) pods in South Kona, Hawaiʻi, but its development was not observed. While we cannot confirm the host relationship in these *S. campanulata*

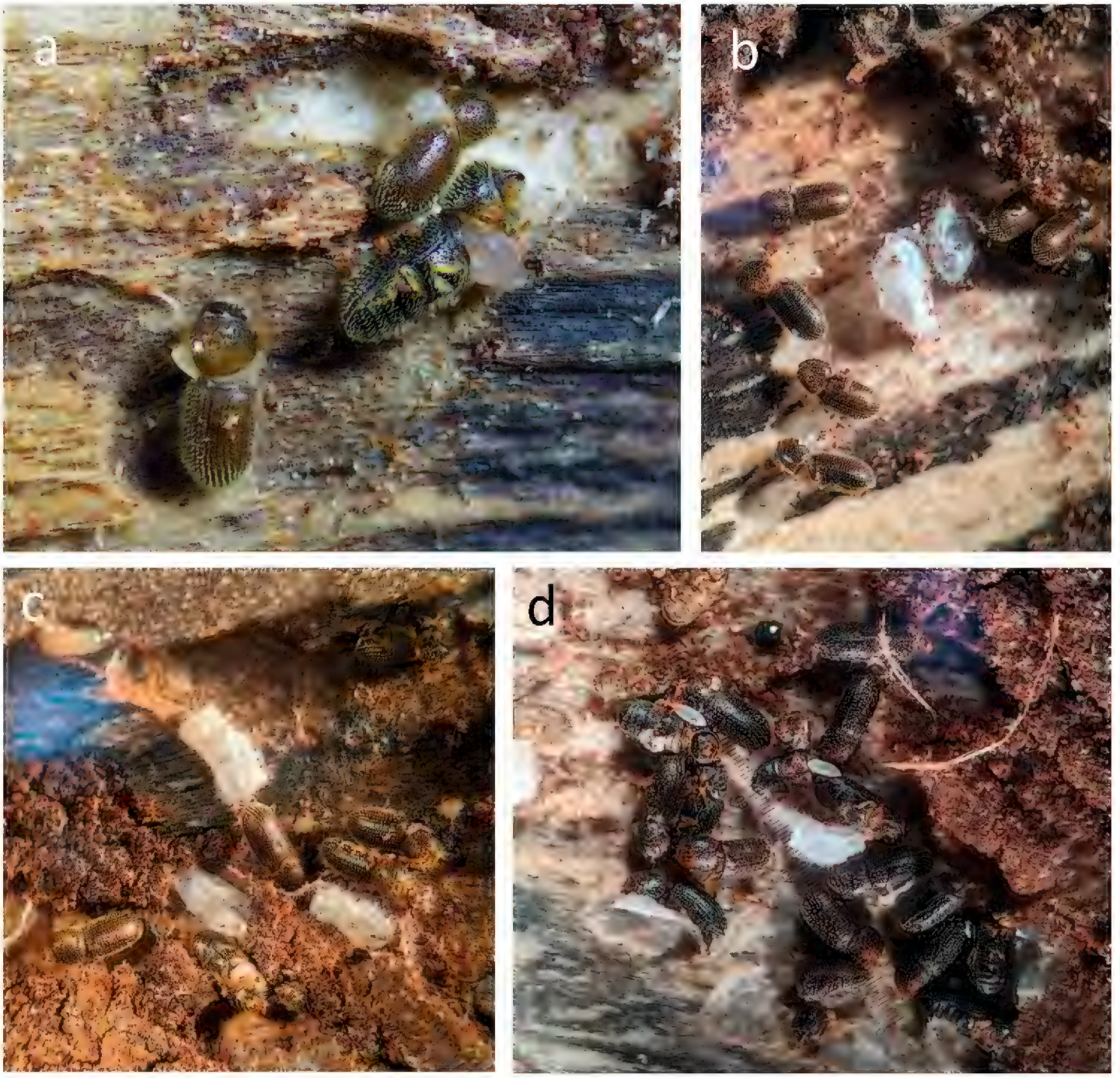


**Figure 6.** *Hypothenemus eruditus* beetles paralyzed and parasitized by *P. maya* or *P. umiehu* in *T. orientalis* branches. All photographs are of naturally occurring situations, taken while peeling bark from branches found in a forested region of Mānoa Valley on Oʻahu (21.3288°N, 157.7930°W, 154 m). Some beetles, such as each of the three in (**a**), are clearly parasitized with a *P. maya* or *P. umiehu* larva feeding through the membranous region of the beetle ventrally between the pro- and mesothorax, the posterior of the larva wrapped around the beetle. All larvae of *P. maya* and *P. umiehu* found in this study were observed to feed in this way. *Prorops* pupae, empty pupal cocoons, and more developing larvae are also visible in (**b,c,d**). Eggs of a thrips species that may scavenge on the remains can also be seen placed on top of beetles in (**d**). All beetles in these pictures were not moving, either paralyzed or killed presumably by *P. maya* or *P. umiehu*. Note that, in contrast to Fig. 8, these photographs are all of *H. eruditus* beetles in unconfined, wide chambers, and thus the development and construction of a pupal cocoon by wasp prepupae does not typically split the beetle into two pieces, and parasitoid pupae are located adjacent to or near the host beetle. It is unknown which of the developing parasitoids in these photographs correspond to which species of *Prorops*, as immatures collected from these branches yielded both *P. maya* and *P. umiehu*.

branches, we presume it also to be attacking *H. eruditus* because this was the only Scolytinae found to be present in the collections from which *P. umiehu* also emerged. Thus there seems to be overlap in host tree and host beetle use between these two species.

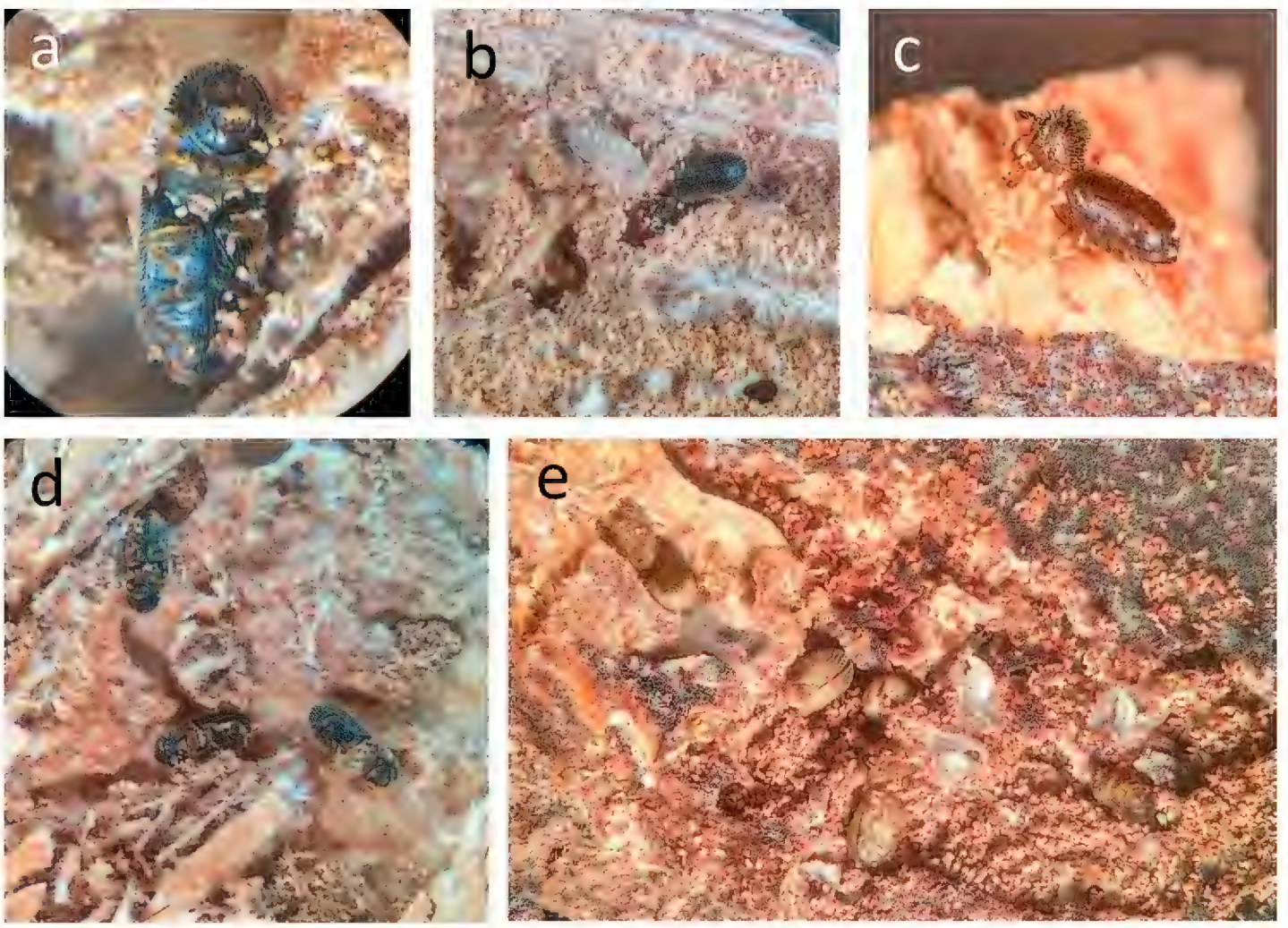


**Figure 7.** *Prorops umiehu* developing immatures. Photographs are of naturally occuring situations, taken while dissecting plant material collected from field environments **a** *P. umiehu* larva on *H. eruditus* from *D. regia* pods collected from the campus of UH Mānoa **b** pupating *P. umiehu* having completed its larval stage on H. *eruditus* in *D. regia* pods from UH Mānoa **c, d** *P. umiehu* larvae on *H. eruditus* from *D. regia* from UH Mānoa **e** macadamia husk from Waimānalo, O'ahu with its inner layer peeled, showing pupating *P. umiehu* having developed on the *H. seriatus* adults next to them.

Notably, *P. umiehu* has not been found parasitizing the related *Hypothenemus* spp. which commonly co-occur with *H. eruditus* in *D. regia* seed pods. Since *H. eruditus* uses many more trees than the three listed above as hosts in Hawai'i, it seems reasonable to assume that both species are associated with more trees than the few listed here.

## Life cycle

Development of *P. maya* and *P. umiehu* immature stages has been observed to occur on *H. eruditus* adult beetles in chambers and galleries the beetles excavate below the surface of the plant material (Figs 6–8). Both species follow a similar pattern. Eggs are laid on the adult beetle on the ventral side of the membranous region of articulation between the prothorax and mesothorax, and the emerging larvae feed on the beetle through the same location. As the developing larva feeds and grows, much of the larva remains outside the beetle and wraps around it, as if the beetle were wearing a necklace, and the anterior of the wasp's body extends further inside the beetle. When feeding by the wasp larva on its host has completed, the larva disconnects from the remains of the beetle and spins an off-white ovoid pupal cocoon in which it pupates.

**Figure 8.** Typical placement of pupae when development occurs in a narrow tunnel environment. The parasitoid larva feeds on the adult beetle through the ventral membranous region between the pro- and the mesothorax. The growth of the larva and its subsequent construction of a pupal chamber forces these two sections of the beetle apart, and pupating larvae are typically found concealed between them. In these pictures, the white material near or around the parasitoid immature is what remains of the pupal cocoon it had constructed after the tunnel was broken open by peeling apart the plant material. Photographs are of naturally occurring situations, taken of plant material collected outdoors **a, b** *Prorops sp.* prepupa (**a**) and pupa (**b**) between two halves of an *H. eruditus* beetle in an *H. eruditus* tunnel in a *T. orientalis* branch collected from Mānoa Valley on Oʻahu; **c:** *Prorops umiehu* pupa in a *D. regia* pod from a tree on the campus of the University of Hawaiʻi at Mānoa. Note the position of the pupal cocoon relative to the beetle in (**c**), not the larva itself which was moved as the pod was peeled apart. Such placement was more common in *T. orientalis* branches where scolytid tunnel systems were often more linear, but atypical in *D. regia* pods possibly due to the less linear and more confused organization of beetle feeding in these pods, but in (**c**) developed in this way due to the topography in the certain section where the beetle was parasitized.

The growth of the larva, positioned as it is, forces the two halves of the beetle apart. If development occurs in a tunnel, there is nowhere for this extra volume to go except to expand along the length of the tunnel. Thus between the growth of the wasp larva, the increased brittleness of the beetle after having been desiccated by the feeding of the larva, and the activity involved in creation of a pupation area by the wasp prepupa, the beetle splits apart and pupating wasps are often found in-between the two parts of the beetle, with the beetle's head and prothorax on one side of the pupating larva and the rest of the beetle on the other (Fig. 8).

Field collections have indicated that oviposition and larval development occurs exclusively on the adult stage of the beetle, and the laboratory tests subsequently described that present *P. maya* and *P. umiehu* adult females with a variety of life stages of *H. eruditus* have resulted in parasitism of only adult beetles. Larval development of laboratory reared *P. umiehu* from egg to adult eclosion is pictured in Fig. 9.

## Behavior observed in field collected plant material

When parasitized beetles were found in *T. orientalis* branches, nearly all the beetles in the gallery were either paralyzed or parasitized (see Fig. 6b–d for examples). In such circumstances, parasitoids on the beetles were close to the same stage of development, and most of

the beetles were dead or paralyzed but not obviously parasitized. This was observed for gallery systems containing developing larvae that yielded *P. maya* (n = 5) and *P. umiehu* (n = 1). Because the density of beetles in these galleries was in the range of that typically observed for surrounding, unaffected gallery systems, this suggests that *P. maya* often attacks nearly all beetles in a host patch. The proportion of adult individuals that were clearly parasitized in a gallery versus dead or paralyzed was recorded on four occasions, with 5/19, 5/6, 3/6, and 5/6 beetles parasitized. Adults of the two *Prorops* spp. were only sometimes found in the galleries with parasitized beetles, implying that adult females of these species do not necessarily remain with their young as do some other bethylids [see for example *Sclerodermus harmandi* (Hu et al. 2012), and *Goniozus nephantidis* (Hardy and Blackburn 1991)]. In the *T. orientalis* branches found to contain these *Prorops* spp., there were often many distinct, unconnected beetle gallery systems in a branch. Wasps or paralyzed beetles were found in very few of these galleries, with the vast majority of galleries inhabited by healthy beetles. This implies that while *P. maya* tends to use nearly the whole host patch within a beetle gallery, most galleries were not utilized by these wasps, and the resulting overall percent parasitism and host mortality in this particular environment was low.

In *D. regia* pods, the pattern of patch use within a gallery system seems to be different. It seems to be much more sparse than in the *T. orientalis* branches, with only a small proportion of individuals in a gallery section either paralyzed or parasitized. This was observed only for *P. umiehu* (n > 15); *P. maya* has thus far only been found in *T. orientalis* branches. While this could be a result of differences in behavior between the two species, it appears more likely that this could be because the geometry of *H. eruditus* gallery systems tends to be different in these two plants. In *T. orientalis* branches, *H. eruditus* use only the thin phloem layer, and tend to construct a somewhat round chamber that extends in two dimensions under the bark, though this chamber eventually branches into a network of tunnels as the second and subsequent generations of beetles develop in the wood. Thus, at least in the earlier stages of beetle activity in the wood, their population tends to be somewhat localized in an uncomplex shape. In *D. regia* pods, the tissue the beetles use as a food source is thick enough relative to the size of the beetles to accommodate movement in three dimensions. Instead of forming a chamber, the beetle galleries take on a topologically more complex pattern, eventually creating a sponge-like network of tunnels spread through the material. The population of beetles inhabiting these tunnels tends to be more spread out within this maze of tunnels. Such variability in the gallery system created by *H. eruditus* among different host plants has been previously reported by Wood (1982) and Browne (1961). The geometry of the host's tunnels may contribute to this difference in patch use patterns, possibly due to the wasps' ability to locate their hosts within them.

## Observation chambers in a laboratory setting

Observed behaviors were largely similar between *P. maya* and *P. umiehu*. While differences in behavior presumably exist, none of the general aspects of behavior and observations recorded here were distinct enough to be clearly associated with one species or the other. Typical observed behavior was as follows, and unless noted otherwise, the below observations apply similarly to both species.

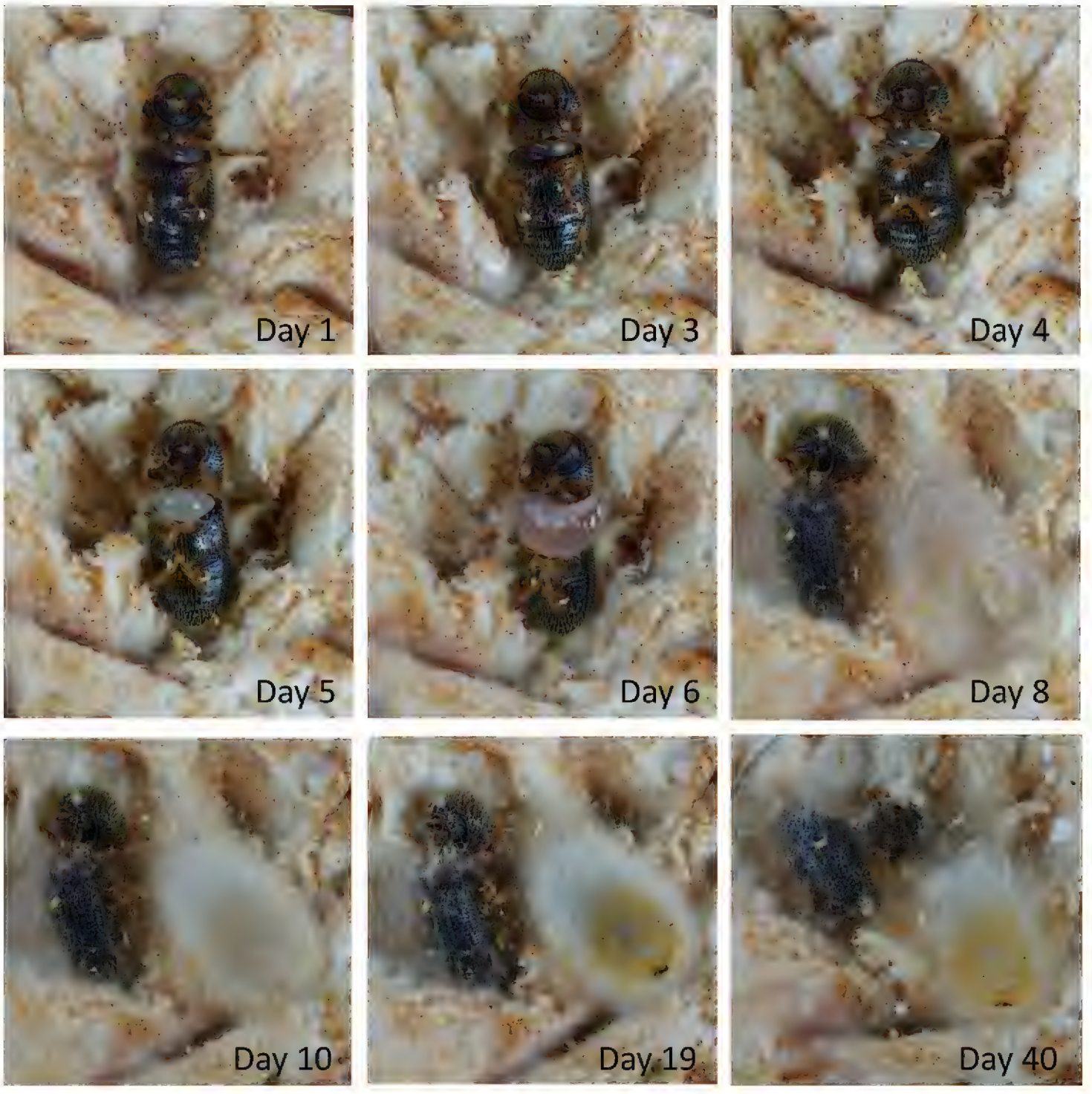


**Figure 9.** Development of *P. umiehu* on *H. eruditus*. The beetle was parasitized by a *P. umiehu* adult female entered into the observation chamber described in the text containing *H. eruditus* beetles on a piece of *D. regia* pod with channels cut into it with a knife. The parasitized beetle was then moved into a small hole carved into a wood substrate and covered with a piece of glass slide cover to mediate humidity and to create an enclosed environment to facilitate construction of a pupal cocoon by the prepupa. Time elapsed after presence of an egg was first observed on the beetle are noted in the photographs. The emerged adult is the allotype.

***General searching behavior*** (Video 1: https://vimeo.com/688211081, Video 2: https://vimeo.com/691136279): The wasps quickly moved through the tunnels in the wood, holding their antennae straight, vibrating and feathering them over the surfaces. This position of the antennae is in contrast to *Allobethylus ewa* (Bridwell, 1920), another bethylid observed in separate studies using the same apparatus, which holds its antennae curved while antennating the surface of a wood substrate or beetles within it, which may function to increase the contact area of the antenna against surfaces with

pits or other irregular texture (D. Honsberger, pers. obs.). The *Prorops* spp. showed clear interest upon finding a beetle, and when immature and adult beetles were present together, the wasps seemed to take preferential interest in the adults, and subsequent stinging, malaxation, chewing, and host feeding behaviors were initially focused on them.

Upon encountering an active *H. eruditus* adult beetle, a female wasp was observed to typically examine and antennate it, often climbing somewhat on top of the beetle in doing so. This was most often followed by an attempt at stinging the beetle, or more rarely, the wasp would either move away and explore elsewhere or repeatedly bite the beetle with its mandibles seemingly with the objective of attempting to move it. Stinging was typically followed by a quick exploration of the beetle and the area around it, and then often by a chewing behavior and host feeding, these actions covered in more detail below. The beetle was typically then abandoned and the wasp moved through the arena and was arrested by the presence of additional beetles on which it performed similar behaviors. Beetles that had previously been stung and paralyzed were often re-encountered by the wasps, who would examine them, occasionally sting them again, and often perform additional chewing or host feeding. *Prorops umiehu*, if taking interest in a larva or pupa, was observed to exhibit a similar progression of stinging and host feeding as with an adult.

The wasps were observed to adeptly turn themselves around in the tight space of a tunnel. Similar behavior has been observed in other parasitoids living in concealed tunnel environments using the same apparatus, such as *Acerocephala hanuuanamu* (Honsberger et al. 2024). As in that species, this maneuver seems to be made possible by the flat shape of the head and the long, articulating prothorax, presumably evolutionary adaptations to moving in tunnel environments. In this maneuver, the wasp ducks its head under its thorax, and follows it with the prothorax, the rest of the mesosoma, and then the flexible abdomen, smoothly sliding over its own body to switch the position of its head and metasoma (Fig. 10e, Video 1: https://vimeo.com/688211081).

***Stinging*** (Figs 10a, b, 11b, c, Video 1: https://vimeo.com/688211081, Video 2: https://vimeo.com/691136279): Initial exploration of an active adult beetle was most often followed by an attempt to sting the beetle, in which the wasp would climb fully on top of the beetle, grip the beetle's elytra or abdomen with its legs, and elongate and arch its metasoma around the beetle and search with its ovipositor for a location on the beetle susceptible to its sting. Crevices in the beetle's morphology encountered by the apex of the abdomen seemed to draw the focus of the exploration, though whether the wasp was able to contact an acceptable part of the beetle with its stinger often seemed more a matter of luck than of planning. A particular preference for aiming at the junction between the pro- and mesothorax was observed, especially evident for *P. umiehu* for which the number of observed stinging events was higher, but attempts were also observed to be made at stinging the ventral side of the abdomen, between the elytra, or the apex of the abdomen for both species. An attempt at stinging was either over quickly and often repeated more than once (though it was unclear if these attempts were successful), or in other cases the behavior persisted for a longer period of up to

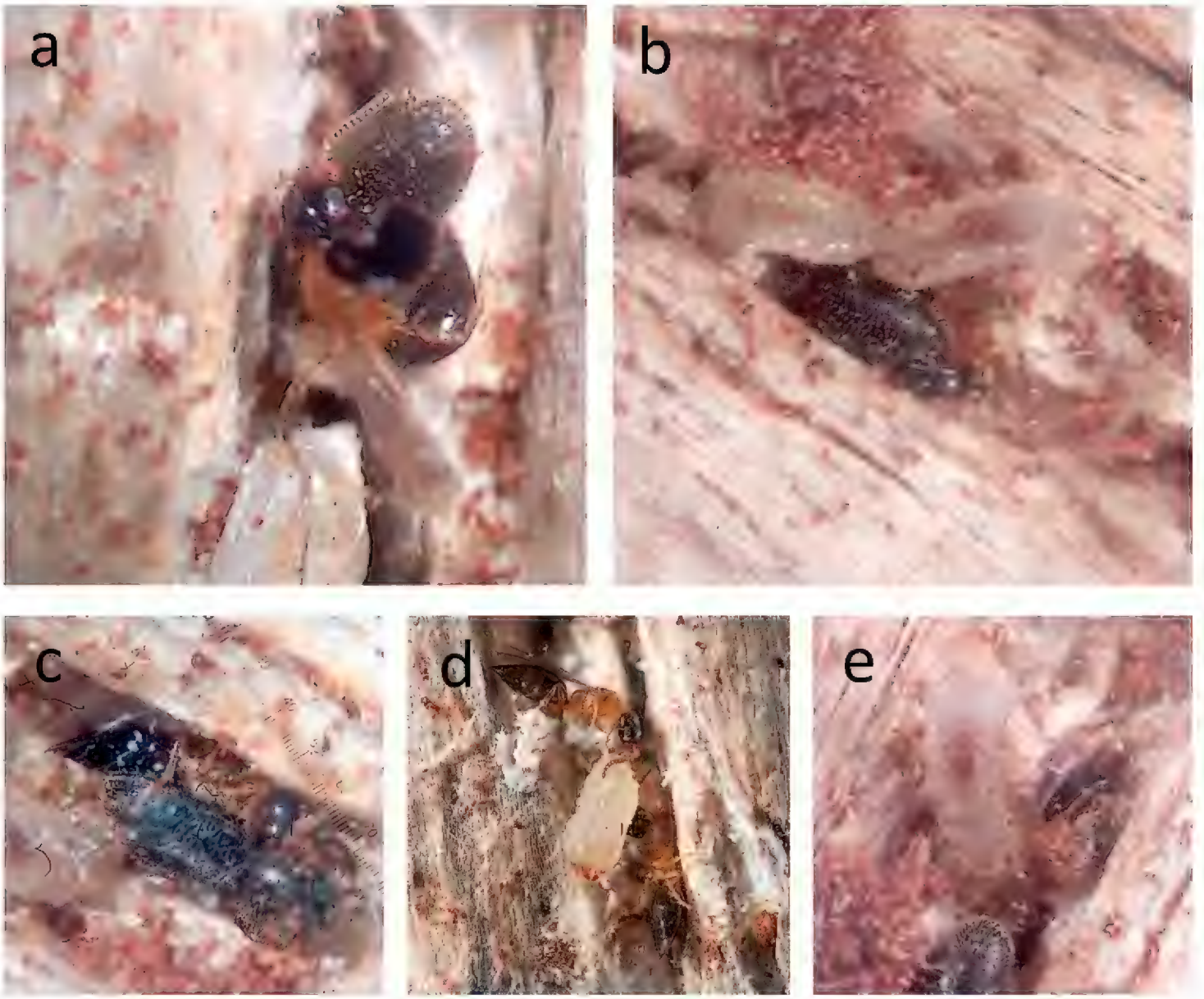


**Figure 10.** Aspects of the behavior of *P. maya* in laboratory observation chambers. The apparatus is the same as in Fig. 11a except using bark peeled from *T. orientalis* branches with channels cut into it with a knife. Beetles are all *H. eruditus*. **a, b** stinging **c** chewing behavior on adult beetle, it was unclear if (**c**) was host feeding or the eventually abandoned preparation of an oviposition site or both **d** host feeding on a larva **e** turning around, reversing the orientation of its body in the tight space of a tunnel. These actions are also shown in Video 1: https://vimeo.com/688211081.

5 minutes. *Hypothenemus eruditus* larvae and pupae were also similarly explored and occasionally stung by both species.

An adult or immature beetle that was successfully stung slowed down over the next few minutes before becoming more or less motionless, making only marginal twitchy movements. After a few days, such subtle twitching movements were still observed, including in beetles having been oviposited on. This implies that the chemicals injected by the wasp are paralytic and do not necessarily kill the beetle. This may maintain the integrity of the nutrition and water content of the beetle as its young develops on it (Vinson and Iwantsch 1980), while preventing the host from dislodging the egg or larva through its movements (Quicke 2015).

***Chewing, oviposition, host feeding, and function of the snout*** (Figs 10c, d, 11e, f, 12; Video 1: https://vimeo.com/688211081, Video 2: https://vimeo.com/691136279,

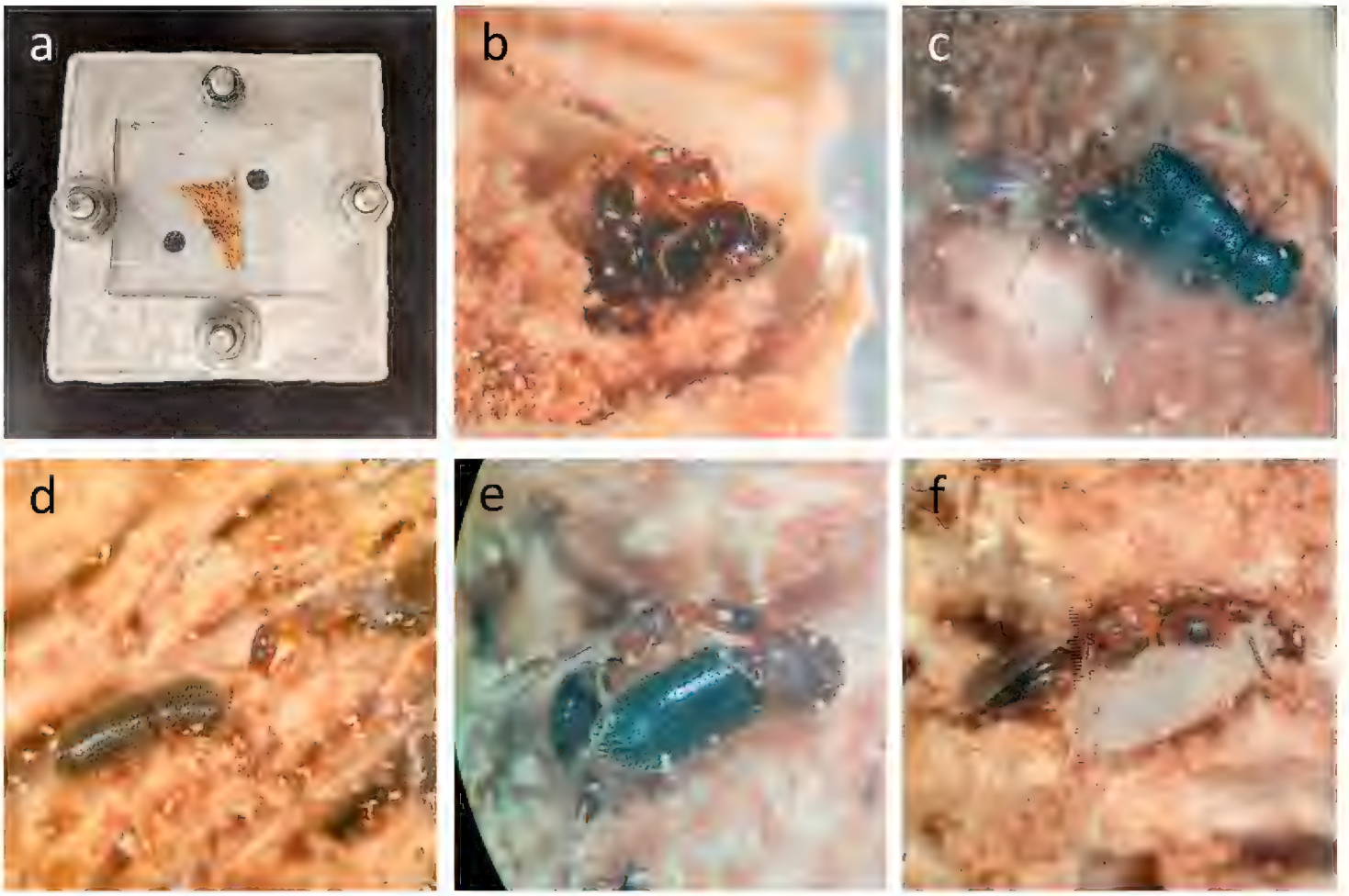


**Figure 11.** Stinging and chewing behavior of *P. umiehu* in laboratory observation chambers **a** the observation chamber used in this study with a piece of *D. regia* pod tissue having been naturally infested by *H. eruditus* sandwiched between the aluminum and plexiglass **b, c** *P. umiehu* stinging *H. eruditus* adult females **d** profile view of a *P. umiehu* female next to *H. eruditus*, showing the groove formed between the snout dorsally and the mandibles ventrally which acts as a mechanism for holding the edge of the prothoracic sclerite of its host **e** the wasp grasps the abdomen of the beetle with its legs and pushes forward on the sclerite with this structure to expose the membranous region between the pro- and mesothorax of the beetle, while maintaining use of the mandibles for chewing on the stretched membrane. This was observed, as in (**e**), for the purposes of host feeding on adults having previously been stung and paralyzed, and was also observed during preparation for oviposition (shown in Fig. 12) **f** host feeding on an *H. eruditus* pupa previously stung and paralyzed. These actions are also shown in Video 2: https://vimeo.com/691136279.

Video 3: https://vimeo.com/688588477): Stinging was often followed by the wasp climbing on top of the lateral or ventral side of the beetle and chewing on the membraneous region between the pro- and mesothorax. This behavior was either abandoned quickly or persisted for extended periods of time, typically in the vicinity of 5 minutes but occasionally as long as 15 minutes. While performing the chewing behavior, the wasp gripped the beetle's abdomen with its legs and pushed the prothorax of the beetle forward using its head, widening the separation between the pro- and mesothoracic sclerites and opening up the membranous region of articulation. The chewing was performed on the stretched membrane at a position as anteriorly advanced as the wasp was able to achieve. In this maneuver, the wasp was able to push on the prothorax by locking the groove formed between the projecting snout and mandibles with the edge of the prothoracic sclerite of the beetle, and in doing so was able to push the sclerite

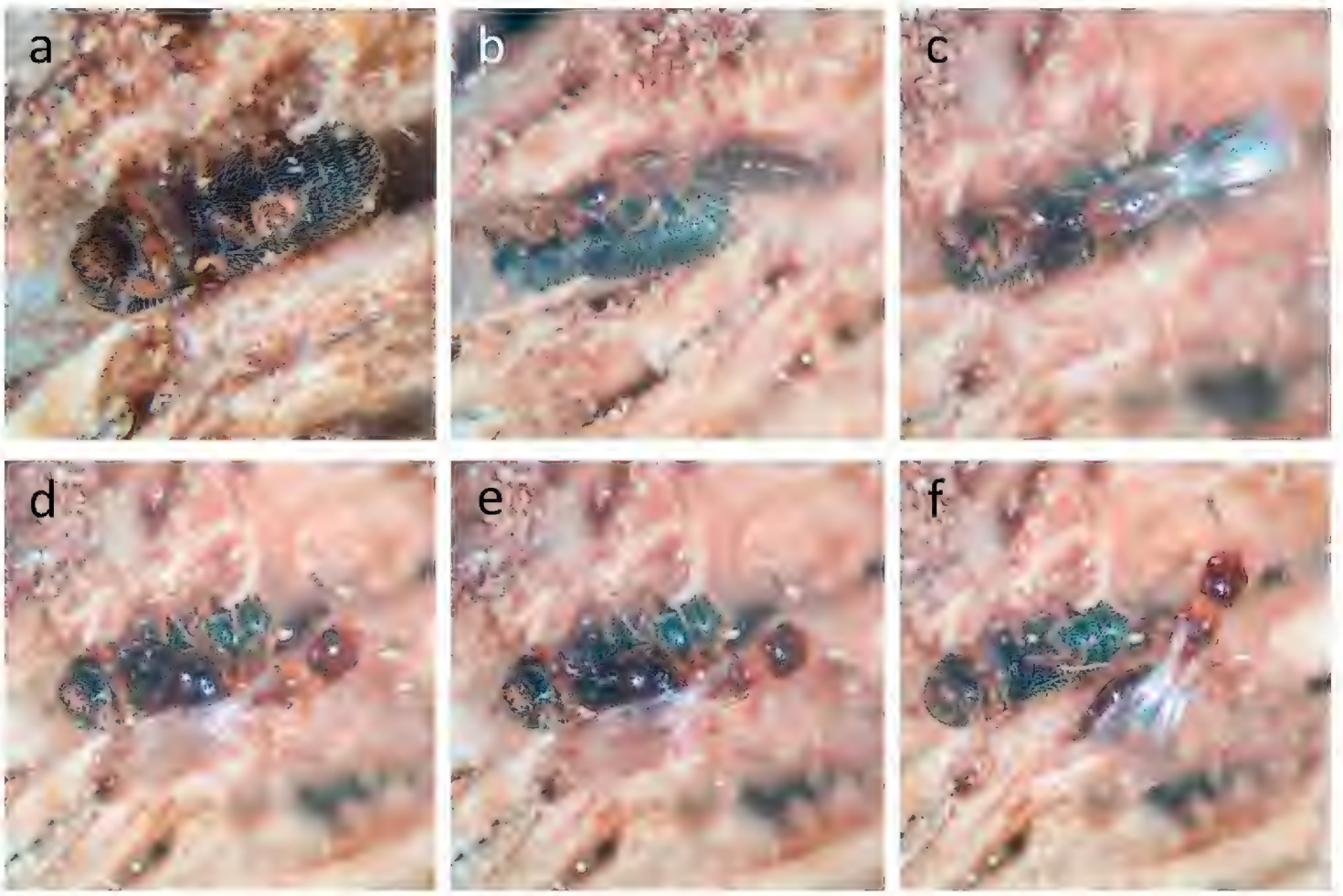


**Figure 12.** Oviposition by *P. umiehu* on *H. eruditus* in a laboratory observation chamber. The apparatus in which this occurred is the same as that pictured in Fig. 11a **a** *H. eruditus* beetle approximately 30 minutes subsequent to oviposition, showing the newly laid egg between the beetle's pro-and mesothorax **b, c** use of the groove between the snout and mandibles in *P. umiehu* to push forward on the prothoracic sclerite of the beetle while chewing on the exposed and tensioned membrane, in preparation for oviposition **d** the wasp then placed the apex of its metasoma between the pro- and mesothorax, into the crevice that remained open as a result of the chewing as in (**b**) and (**c**), and maintained that position for approximately 10 minutes **e** the wasp slowly draws her metasoma across the crevice while the egg exits **f** the host, wasp, and egg subsequent to completion of oviposition. These actions are also shown in Video 3: https://vimeo.com/688588477.

forward without it sliding over the wasp's face while maintaining use of its large mandibles for chewing. This chewing action functioned as the method of host feeding on adult beetles and was also performed in preparation for oviposition.

All eggs observed both in the laboratory observation chambers and field collected wood from both species were placed at the same location on the adult beetles: transversely oriented on the ventral side of the membraneous region of articulation between the pro- and mesothorax. Thus one use of the chewing behavior was apparently to prepare the host for oviposition, though its exact function was not clear: it could possibly be to cut the membrane so that the gap between the pro- and mesothorax would remain open and present an accessible area for oviposition and egg development; to cut open the tissue so that the emerging larva would be able to penetrate the membrane and feed; to cut the ventral nerve cord; for the adult to taste the beetle's hemolymph to assess its quality as a host; or alternatively, simply for the adult to host feed on the

beetle. Adult *Sclerodermus harmandi* (Buysson, 1903) (Hym.: Bethylidae) have been observed to chew holes through the cuticle of their host larvae through which their offspring feed as larvae (Hu et al. 2012)

The act of oviposition (Video 3: https://vimeo.com/688588477) was only observed once, for *P. umiehu*. An *H. eruditus* adult previously stung, paralyzed, and likely chewed on as evidenced by the separation between the pro- and mesothorax greater than normal for a beetle that had simply been stung, was approached by the wasp and its actions were observed for the 2.5 hours leading up to oviposition. In this time, the wasp initially explored the beetle and the surrounding area, focusing much of its attention near the junction of the pro- and mesothorax, and attempted to subtly manipulate the beetle's position in the tunnel by grabbing the body of the beetle with its mandibles. The wasp then remained motionless in the tunnel, its body oriented opposite that of the beetle, the two touching head to head. This was followed by a short chewing interval, after which the wasp reassumed its position motionless in the tunnel with the beetle for approximately 1.5 hours. The wasp then resumed its exploration of the beetle, short chewing intervals, and subtle manipulations of the beetle's position, followed by an extended chewing event on the membrane along the midline of the beetle. It then explored the area and the beetle, repeating short but vigorous chewing intervals. The wasp then after a few attempts grabbed the beetle and repositioned it approximately a body length away in a slightly wider section of the tunnel. This was followed by one more vigorous chewing event, after which the wasp turned around and reached the apex of her metasoma into the gap between the pro- and mesothorax. The wasp remained in this position for about 10 minutes, her metasoma pulsating slightly. Then, over about 30 seconds, the wasp slowly moved the apex of her metasoma transversely across the crevice and the egg was visible emerging. The wasp slowly withdrew and became active again, exploring the vicinity for a few minutes and then left the area. The next day, the wasp was observed again in the tunnel in the same position as that in which it had remained motionless for extended intervals prior to oviposition, this time for at least 30 minutes as if host guarding, but did not maintain that position.

The chewing behavior was commonly observed on paralyzed adult beetles for both *Prorops* spp., and in the vast majority of observed instances were not followed by oviposition. Many of these interactions seemed to be for the purpose of host feeding, but it was unclear if some also were for the purpose of oviposition but on a host that was eventually rejected. Chewing by both species was also observed to occur on immature stages that had previously been stung. Since no eggs or developing larvae were ever observed on an immature stage, chewing on pupae and larvae was presumably not for the purpose of oviposition, but instead for host feeding.

***Intraspecific interactions*** were also observed. When encountering each other in open space, the wasps typically ignored each other. Females in the action of stinging or chewing were typically not interrupted by passing conspecifics, which might explore the beetle with their antennae. They were observed to be somewhat affected, though not to show any overt aggression, if both were exploring the same beetle adult or immature: if the wasps came in contact with each other, they would move slightly apart.

***Defense against stinging by a* Hypothenemus *sp.*** (Fig. 13, Video 4: https://vimeo.com/688212175): An unidentified *Hypothenemus* sp. male, not *H. eruditus* but similar in size to *H. eruditus* females, was placed in the observation chamber along with *H. eruditus* beetles. In a behavior not observed in *H. eruditus* beetles under the same circumstances, when a *P. umiehu* adult female attempted to sting the *Hypothenemus* sp. adult dorsally between the pro- and mesothorax, the beetle clamped down at this junction on the apex of the wasp's abdomen as soon as it made contact. The wasp did not seem to become agitated, but when appearing to attempt to withdraw after 1.5 minutes, a time in the range of a normal stinging interval, seemed to struggle and was unable to extract its metasoma from the grasp of the beetle until it relaxed 3.5 minutes later. The beetle seemed to be unaffected by the stinging attempt and remained active through the next day. It was unclear if the beetle was not paralyzed because *P. umiehu* is not physiologically able to paralyze this species, or was a result of this behavior which resulted in an unsuccessful stinging attempt. This behavior was only observed once. The wasps for the most part showed little interest in this species when they were placed in the arena and focused their attention on *H. eruditus*. Aside from this observation, neither this *Hypothenemus* sp. nor *H. eruditus* were observed to present other active forms of defense, such as running away or biting, against the wasps.

***Patch use*:** Almost all beetles entered into the observation chambers with *P. maya* or *P. umiehu* females were motionless within 12 hours (n = 3 for *P. maya*, n = 3 for *P. umiehu*), helping to confirm the observation in field collected wood that *P. maya*, and potentially *P. umiehu* as well, typically attacks more or less the whole

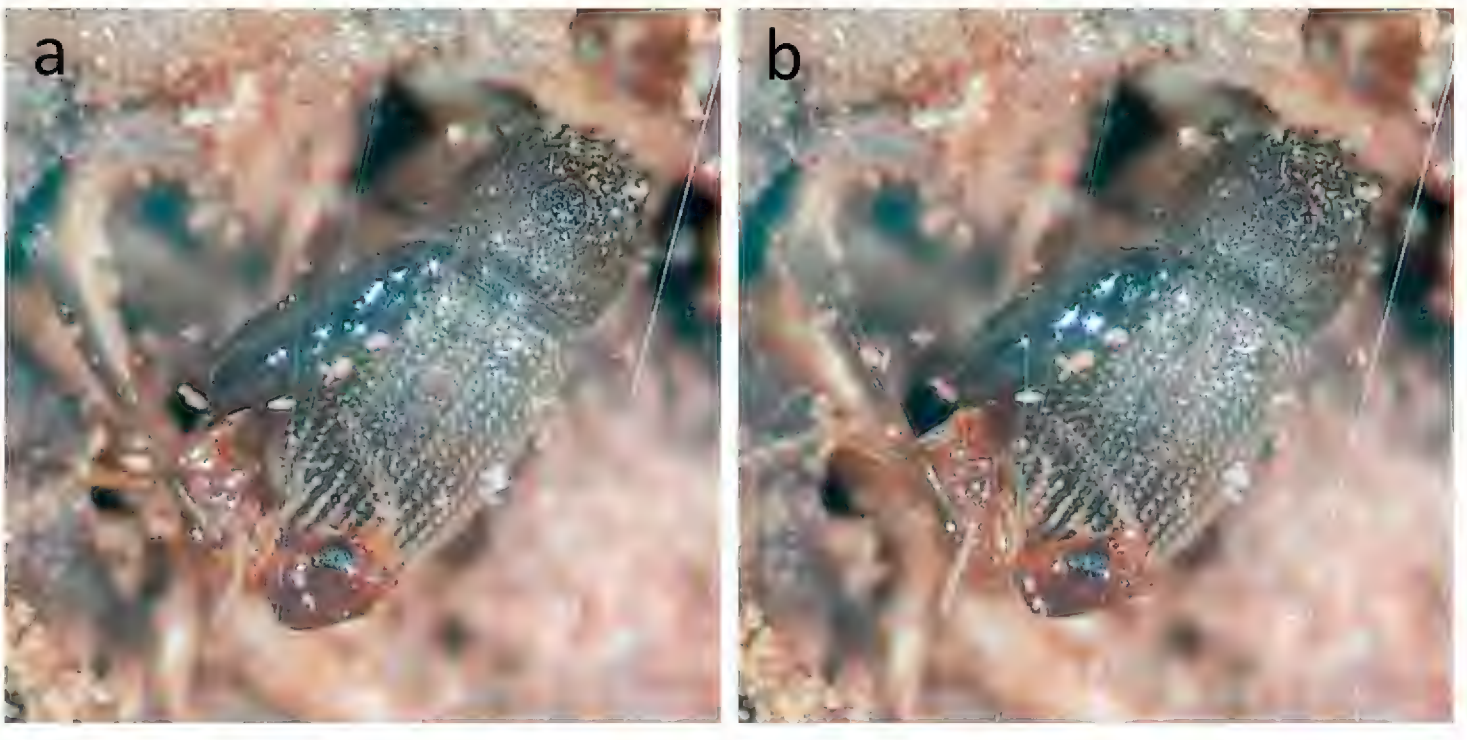


**Figure 13.** Defense by *Hypothenemus* sp. male against a stinging attempt by *P. umiehu*. The identity of the beetle is unknown, but is not *H. eruditus* **a** position immediately prior to contact of stinger. Note that the beetle is in a relaxed state, with the gap between the pro- and mesothorax slightly open **b** The beetle quickly clamps down after contact, trapping the apex of the metasoma of *P. umiehu*, and maintains that position for approximately 3.5 minutes, during which time the wasp was not visibly agitated but was unable to extricate itself. The beetle appeared to remain healthy and active in the subsequent hours, seemingly unaffected by the stinging attempt. These actions are also shown in Video 4: https://vimeo.com/688212175.

host patch at least in geometrically simple environments such as those with which they were presented. In one instance where the details were more precisely recorded, five *H. eruditus* and the one unidentified *Hypothenemus* sp. male which showed the defensive behavior were inserted into the observation chamber in naturally bored *H. eruditus* galleries in *D. regia* pods with two *P. umiehu* adult females. All five *H. eruditus* were stung and paralyzed within two hours.

### Interest in *Hypothenemus hampei*, the coffee berry borer?

Given that the congeneric *Prorops nasuta* is a parasitoid of the coffee berry borer *H. hampei*, and of the known species of *Prorops* it seems close at least morphologically to *P. maya* females, and *H. eruditus* and *H. hampei* are also congenerics, we investigated whether *P. maya* would take any interest in the coffee berry borer. To test this, wasps were released into the same apparatus described above that successfully resulted in stinging, chewing, host feeding, and parasitism of *H. eruditus*, with *H. eruditus* adults and immatures switched out with *H. hampei* adults and immatures (Video 5: https://vimeo.com/691136424). No interest was observed, and the wasps even seemed to show slight repulsion, upon encounter briefly antennating the beetles and then quickly moving on. No stinging, chewing, host feeding, or parasitism was observed. Given this lack of interest, no further tests were done.

## Discussion

*Prorops maya* and *P. umiehu* are ectoparasitoids of adult *H. eruditus* beetles living below the surface of wood. Both species enter tunnels bored by the scolytid in the plant material, and sting, paralyze, oviposit, and develop as an ectoparasitoid on the adults. *Prorops maya* and *P. umiehu* are, as far as we are aware, along with a *Plastanoxus* sp. found to parasitize *Euwallacea fornicatus* by Husein et al. (2023), the only bethylids known to parasitize the adult stage of their host, and the only known ectoparasitoids of the adult stage of a scolytid.

### Notes on the life history and morphology of *P. maya* and *P. umiehu*

The vast majority of parasitoids of Scolytinae whose biology are known reproduce only on immature host stages (Kenis et al. 2007). Intuitively, this makes sense because larvae and pupae are much less mobile and sclerotized than adults, and often found at the end of a one-way tunnel. So why might a parasitoid attack the adult stage? It may be advantageous as an escape from competition with other parasitoids or predators; it may be because adult scolytids might be present in gallery systems more consistently than immature stages if their reproduction occurs only intermittently; or because of accessibility to adults for a cryptoparasitoid given their location within galleries, at entrances or in larger diameter tunnels. Development as an endoparasitoid inside the sclerotized adult stage may also offer protection from predators or hyperparasitoids, though endoparasitic development often also comes at the expense of having to de-

fend against the host's immune system (Godfray 1994). *Prorops maya* and *P. umiehu* develop as ectoparasitoids on *H. eruditus* adults, but seem to have evolved a way of still using their host to protect themselves, at least when developing in a tunnel system. In such environments, *P. maya* and *P. umiehu* were observed to pupate between the prothorax and posterior of the beetle, having forced the two halves of the beetle apart during its growth and subsequent construction of a pupation chamber. This may be an adaptation to use the sclerotized body of its host to protect itself as best as it can given the potential evolutionary constraint of being an ectoparasitoid characteristic of Bethylidae, and maintaining the advantage of reduced exposure to the host's immune system inherent in being an ectoparasitoid.

Because *P. maya* and *P. umiehu* were found parasitizing nonnative beetles in nonnative trees, the host beetles in a tribe with no native species, and *Prorops* is not otherwise known in Hawai'i, Hawai'i is not likely part of the native range of either species. It may also be unlikely the native host of these species is *H. eruditus*: their pattern of host use was not observed to be efficient and *H. eruditus* showed a lack of defensive behavior against attack, while potentially effective defensive behavior was shown in another *Hypothenemus* sp.

While *P. maya* seemed to parasitize or paralyze nearly every *H. eruditus* beetle in a gallery system in *T. orientalis* branches, most unconnected active beetle gallery systems in a contiguous piece of wood appeared untouched, containing healthy populations of beetles. Because the environment where we have observed this species is likely not its native environment, to which it is presumably best adapted, such sparse host use could potentially result from inefficient searching behavior due to lack of adaptation to the exact host or environmental cues present. Or, possibly, this sparse and spatially disparate use of galleries could result from adaptation to an environment where its natural enemies tend to search in a spatially contiguous manner, *e.g.* by walking along a branch. Observed sporadic gallery use could also be related to low population density of the parasitoids, and restricting oviposition to a single gallery system and incapacitating all other occupants could also be related to brood guarding, though such behavior was not convincingly observed for these species.

Finally, we make a note about morphology. *Prorops* is the only genus in Sclerodermi-nae with a projection on its frons, a synapomorphy that can be used to identify the genus. This, in combination with the large mandibles, has previously been suggested to possibly function as a means of digging through hard substrate (Waichert and Azevedo 2012). Of the three species in *Prorops* for which the biology is known, *P. maya* and *P. umiehu* are parasitoids of the adult stage of beetles, and *P. nasuta* is a parasitoid of the larval and pupal stages. Thus it may be that parasitism of the adult stage is more representative of the genus as a whole than parasitism of immature stages. For many ectoparasitoids of larvae and pupae, which have a cuticle almost entirely soft and easy to penetrate by an emerging parasitoid larva, the exact location of placement of the egg on a paralyzed host does not matter greatly. The location of egg placement on the host may matter more for parasitoids of adult beetles, which are sclerotized and have a cuticle not as easily penetrated. All eggs observed in this study were placed in the same location on the beetle, on the membraneous region of articulation between the pro- and mesothorax on the ventral side

of the beetle. In preparation for oviposition, and in host feeding, *P. maya* and *P. umiehu* were observed to widen the separation between the pro- and mesothorax of the beetle by grasping the host beetle's abdomen with its legs and pushing the pronotal sclerite forward with its head. This was accomplished by fitting the edge of the pronotal sclerite into the groove formed between the mandibles ventrally and the snout dorsally, using this structure as a locking mechanism to hold the sclerite and push it forward while maintaining use of the mandibles for chewing on the exposed and tensioned membrane. Among possible other functions, this chewing presumably cuts the stretched membrane and results in the space between the pro- and mesothorax remaining open upon cessation of pushing by the wasp. For oviposition, the female wasp subsequently inserts the apex of its metasoma into this widened gap and lays an egg into it. The cut membrane may presumably also provide an opening through which the emerging larva is able to feed, and allows the wasp to host feed on the beetle. Alternatively, the snout could have evolved for host feeding on adults even if parasitism occurred only on immature stages. Given its variety of forms within the genus and apical dorsad curvature in both species considered here, which would appear possibly as a prying or positioning mechanism, the snout structure in *Prorops* may have additional uses as well that were not observed during this study. But the conferred ability to hold the prothorax of an adult host beetle and push on it, for the purpose of host feeding and in preparation for oviposition, represents one function.

## Data availability

Additional video materials: Video 1: Searching, stinging, chewing, and host feeding behavior by *Prorops maya* on *Hypothenemus eruditus*: https://vimeo.com/688211081; Video 2: Searching, stinging, chewing, and host feeding behavior by *P. umiehu* on *H. eruditus*: https://vimeo.com/691136279; Video 3: Oviposition by *P. umiehu* on *H. eruditus*: https://vimeo.com/688588477; Video 4: Defense by *Hypothenemus* sp. male against a stinging attempt by *P. umiehu*: https://vimeo.com/688212175; Video 5: Response of *P. maya* to the coffee berry borer, *H. hampei*: https://vimeo.com/691136424.

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